Moss Flora of Central America

Part 3. Anomodontaceae–Symphyodontaceae

Bruce Allen

Central America is a small region (three-fourths the size of Texas) with one of the most diverse moss floras of any area of the world. The mosses of Central America are not especially endemic, but rather represent an eclectic moss flora produced by the pronounced vertical relief of the region and its close physical position to three species-source areas: South America, North America, and the Caribbean. In addition, many species from Africa and Southeast Asia are found in the region. Central America as here delimited is political; it includes all parts of Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama. The *Moss Flora of Central America* is a four-part, revisionary flora. Parts 1–3 of the *Flora* treated 760 species; part 4 will treat 213 species. This volume gives keys, descriptions, and discussions for 239 of the 973 moss species. In addition, for each species precise type information is provided; distribution within Central America is documented by the examination of specimens; world distribution is indicated; habitat notes based on personal field experience or taken from collection labels are provided; and a list of previously published illustrations is given. Beginning with part 2, all species included in the *Flora* are illustrated by means of black-and-white line drawings.

Moss Flora of Central America

Political subdivisions are numbered more or less from left to right in each country.

Most inland bodies of water and offshore islands are not shown in this sketch map.

Approximate scale: 200 km

Mexico

Belize
- 3, Belize
- 4, Cayo
- 1, Corozal
- 2, Orange Walk
- 5, Stann Creek
- 6, Toledo

Honduras
- 2, Atlántida
- 17, Choluteca
- 3, Colón
- 9, Comayagua
- 8, Copán
- 1, Cortés
- 15, El Paraíso
- 10, Francisco Morazán
- 4, Gracias a Dios
- 13, Intibucá
- 14, La Paz
- 12, Lempira
- 11, Ocotepeque
- 7, Olancho
- 5, Santa Bárbara
- 16, Valle
- 6, Yoro

Nicaragua
- 10, Boaco
- 14, Carazo
- 1, Chinandega
- 13, Chontales
- 4, Estelí
- 12, Granada
- 5, Jinotega
- 7, León
- 3, Madriz
- 9, Managua
- 11, Masaya
- 8, Matagalpa
- 2, Nueva Segovia
- 15, Río San Juan
- 16, Rivas
- 6, Zelaya

Panama
- 1, Bocas del Toro
- 4, Canal Area
- 6, Chiriquí
- 8, Coclé
- 3, Colón
- 10, Darién
- 7, Herrera
- 11, Los Santos
- 9, Panamá
- 5, San Blas
- 2, Veraguas

Guatemala
- 4, Alta Verapaz
- 8, Baja Verapaz
- 13, Chimaltenango
- 16, Chiquimula
- 9, El Progreso
- 20, Escuintla
- 14, Guatemala
- 2, Huehuetenango
- 5, Izabal
- 15, Jalapa
- 22, Jutiapa
- 1, Petén
- 11, Quetzaltenango
- 3, Quiché
- 17, Retalhuleu
- 19, Sacatepéquez
- 6, San Marcos
- 21, Santa Rosa
- 12, Sololá
- 18, Suchitepéquez
- 7, Totonicapán
- 10, Zacapa

El Salvador
- 7, Ahuachapán
- 3, Cabañas
- 2, Chalatenango
- 11, Cuscatlán
- 9, La Libertad
- 12, La Paz
- 6, La Unión
- 5, Morazán
- 4, San Miguel
- 10, San Salvador
- 13, San Vicente
- 1, Santa Ana
- 8, Sonsonate
- 14, Usulután

Costa Rica
- 2, Alajuela
- 7, Cartago
- 1, Guanacaste
- 3, Heredia
- 4, Limón
- 5, Puntarenas
- 6, San José

Cocos Island
500 km

Colombia

Copyright © Missouri Botanical Garden

4329.FloraCentAmer.Endsheet.indd 1 8/30/10 2:18:43 PM

Moss Flora of Central America

Part 3. Anomodontaceae–Symphyodontaceae

Moss Flora of Central America

Part 3. Anomodontaceae–Symphyodontaceae

Bruce Allen
with contributions from
Ronald A. Pursell
Robert R. Ireland

MISSOURI BOTANICAL GARDEN

MONOGRAPHS IN SYSTEMATIC BOTANY FROM THE MISSOURI BOTANICAL GARDEN

Volume 117

Published on 10 September 2010 in an edition of 500 copies

ISSN 0161-1542
ISBN 978-1-930723-95-5
Library of Congress Control Number: 94225522

Author's addresses

Bruce Allen
Missouri Botanical Garden
P.O. Box 299
St. Louis, Missouri 63166-0299

Ronald A. Pursell
Biology Department
Pennsylvania State University
University Park, Pennsylvania 16802

Robert R. Ireland
Smithsonian Institution
NMNH, Department of Botany
MRC-166
P.O. Box 37012
Washington, D.C. 20013-7012

SCIENTIFIC EDITOR AND HEAD
Victoria C. Hollowell

MANAGING EDITOR
Beth Parada

ASSOCIATE EDITOR
Allison Brock

ASSOCIATE EDITOR
Tammy M. Charron

PRESS COORDINATOR
Cirri R. Moran

TECHNICAL EDITOR FOR THE VOLUME
Diana Gunter

Copyright © 2010 by Missouri Botanical Garden Press
P.O. Box 299
St. Louis, Missouri 63166-0299, U.S.A.
www.mbgpress.org

All rights reserved. Printed in U.S.A.

To my mother, Jane Elizabeth Palmer Allen
(2 December 1924 – 27 April 2005)

You are right in thinking I work hard. This I do to keep alive:
for nothing resembles death so closely as idleness.

— Frederick the Great

Contents

Introduction ix
Acknowledgments ix
New nomenclature x
Moss Flora of Central America
Anomodontaceae 1
Hedwigiaceae 16
Rhacocarpaceae 31
Cryphaeaceae 38
Forsstroemiaceae 74
Leucodontaceae 78
Lepyrodontaceae 85
Prionodontaceae 90
Meteoriaceae 100
Lembophyllaceae 169
Pterobryaceae 182
Phyllogoniaceae by Ronald A. Pursell 252
Catagoniaceae 262
Neckeraceae 266
Porotrichodendron by Robert R. Ireland & Bruce Allen 315
Pilotrichaceae 363
Daltoniaceae 386
Hookeriaceae 432
Leucomiaceae 676
Hypopterygiaceae 693
Symphyodontaceae 699
Literature Cited 703
Index 715

Introduction

This third part of *The Moss Flora of Central America* treats 237 species and varieties of mosses in the families Anomodontaceae through Symphyodontaceae. The first part of this Flora treated 208, while the second part treated 313, species and varieties. This Flora is specimen-based, and wherever possible type specimens have been examined. In this volume particular care has been given to the citation of types; for every taxon the specimen information given in the original protologue is exactly repeated. This information is preceded by an indication of the country of origin of the type specimen (in square brackets) if the country is not evident from information given in the specimen protologue. When type material for a particular taxon has been examined, the protologue information is followed by a statement that exactly repeats the label information on the type specimen. All examined type material within the text is followed by the citation of an *Index Herbariorum, Ed. 8* acronym at the end of the type specimen information.

As much as possible, the generic keys and descriptions refer to the genera as a whole and not just to the species found in Central America. To facilitate use, the genera are arranged alphabetically within families and the species alphabetically within genera. Generic and species descriptions, as well as the discussions, in Part 3 are often longer and more detailed than those given in previous parts of the Flora. Each species in Part 3 is illustrated with a full plate of figures that includes habit drawings as well as microscopic features; in addition a list of previously published illustrations for each species is given. Short, concise habitat notes based on my field experience with the species or taken from specimen labels follow the citation of illustrations. The Central American distribution of all species is determined by the examination of specimens. All species for which a specimen cannot be located are placed in "Species Excluded" sections. In a few cases mosses so far only found in other nearby regions, such as the Caribbean or South America, have been included in the treatment. The distribution of species within each country is documented by the citation of one specimen from each political unit (department, district, or province) in which the species occurs. Quetzaltenango, the modern spelling for this Guatemalan Department, is used in this volume rather than the form (Quezaltenango) used in previous volumes of this series. An indication of the world range of each species is given either based on the examination of specimens or extracted from reliable literature reports. The system put forward by the *World Geographical Scheme for Recording Plant Distributions* (Brummitt 2001) is the main one used for citing world ranges. Within the citations only the regional groups are named, and they are arranged into continental groups that are set off from each other by semicolons. There are three exceptions to the Brummitt (2001) scheme: Mexico, Central America, and the Caribbean are treated as continental rather than regional groups and are set off by semicolons. In Brummitt (2001) Mexico is part of Northern America, while Central America and the Caribbean are part of Southern America.

Acknowledgments

National Science Foundation grant DEB-0072433 to the Missouri Botanical Garden financially supported work on the *Moss Flora of Central America*. National Geographic Society grants 4556-91 to Gerrit Davidse and 5172-94 to Randall Evans supported field work in Honduras. National Geographic Society grant 5634-96 to Bruce Allen and Alan Whittemore supported field work in Belize. I am indebted to Thomas Hawkins for his assistance in nearly all aspects of my field work in Honduras and Belize. I thank Marshall R. Crosby for his support and encouragement of this project; I am especially grateful for his excellent Central American moss collections, which have greatly improved the Flora. I am greatly indebted to William R. Buck for his taxonomic and nomenclatural advice throughout this project; help in locating type or other critical specimens in the New York Botanical Garden herbarium; the use of his extensive slide collection; and his careful, critical reading and commenting on the final draft of this part of the Flora. I thank Diana Gunter for copyediting the manuscripts, Beth Parada for her support during editing and production, and Victoria Hollowell for facilitating the timely publication of this volume.

Forsstroemiaceae B. H. Allen, *stat. et comb. nov.*
Sphaerotheciella macrospora (Herzog) B. H. Allen, *comb. nov.*
Sphaerotheciella gracillima (Herzog) B. H. Allen, *comb. nov*.
Barbellopsis macroblasta (Broth.) B. H. Allen, *comb. nov.*
Orthostichopsis fornicata B. H. Allen & W. R. Buck, *sp. nov.*
Pireella crosbyi B. H. Allen, *sp. nov.*
Pireella hondurensis A. E. Newton & B. H. Allen, *sp. nov.*
Porotrichum evansii B. H. Allen, *sp. nov.*
Brymela angustiretis (E. B. Bartram) B. H. Allen, *comb. nov.*
Brymela complanata B. H. Allen, *sp. nov.*
Brymela crosbyi (B. H. Allen) B. H. Allen, *comb. nov*.
Brymela laevinervis (Renauld & Cardot) B. H. Allen, *comb. nov.*
Callicostella callicostelloides (Herzog & Thér.) B. H. Allen, *comb. nov.*
Cyclodictyon crosbyi B. H. Allen, *sp. nov.*
Cyclodictyon validirugosum B. H. Allen, *sp. nov.*
Lepidopilum exiguum B. H. Allen, *sp. nov.*
Lepidopilum ultramarginatum B. H. Allen, *sp. nov.*
Stenodictyon crosbyi B. H. Allen, *sp. nov.*
Stenodictyon ovatum B. H. Allen, *sp. nov*.
Thamniopsis colombica (R. S. Williams) B. H. Allen, *comb. nov*.
Thamniopsis glandulifera (Hampe) B. H. Allen, *comb. nov.*
Thamniopsis guatemalensis (E. B. Bartram) B. H. Allen, *comb. nov*.
Thamniopsis oedodontia B. H. Allen, *sp. nov*.
Thamniopsis rivularis (Mitt.) B. H. Allen, *comb. nov.*
Thamniopsis standleyi (E. B. Bartram) B. H. Allen, *comb. nov.*
Thamniopsis steyermarkii (E. B. Bartram) B. H. Allen, *comb. nov.*
Trachyxiphium repens (Hook. & Grev.) B. H. Allen, *comb. nov.*

ANOMODONTACEAE

Anomodontaceae Kindb., Gen. Eur. N.-Amer. Bryin. 6. 1897.

Plants small, medium-sized or robust, in cushions, tufts, or mats on rocks or trees. Primary stems creeping; leaves reduced, often widely spaced; rhizoids red brown, in moderate-sized clusters at abaxial side of leaf insertions, not or weakly and irregularly branched. Secondary stems erect, erect-ascending, or loosely spreading, simple or variously branched, secondary stems and branches at times transformed at the tips into stolons or flagellate branches; cross section with sclerodermis, cortical cells enlarged, central strand present or absent; paraphyllia absent; pseudoparaphyllia present or absent. Secondary stem and branch leaves similar or differentiated, decurrent or non-decurrent; apices acuminate, acute, or broadly rounded to obtuse; margins plane, erect, or recurved; costae single, strong, reaching beyond midleaf, often wavy above, in cross section cells homogeneous, thick-walled; cells quadrate, rounded-quadrate, subquadrate, oblate, or irregularly hexagonal, smooth, bulging-mammillose or densely pluripapillose, juxtacostal cells near the insertions differentiated. Dioicous. Setae elongate. Capsules erect, more or less symmetric, globose, oblong-ovate, or elliptic; stomata present or absent; opercula obliquely or straight conic-rostrate to rostrate; annuli rudimentary or compound; peristome double; exostome teeth white to yellow, at times reddish orange at base, narrowly triangular to linear, dorsal (outer) surface papillose-striate at base and papillose above or throughout, trabeculae variously projecting; endostome papillose, to 3/4 the exostome length or rudimentary, segments narrow and perforate or reduced to stubs, basal membranes low, cilia rudimentary or absent. Spores papillose. Calyptrae cucullate, smooth or sparsely hairy.

The Anomodontaceae were established by Buck and Vitt (1986) for a group of genera with prostrate, sympodial branched, primary stems, short leaf cells, and narrow, often white, papillose exostome teeth. They placed the family in the Leucodontales, near the Cryphaeaceae. Of these features only its sympodial branched, prostrate primary stems are germane to a consideration of its familiar relationships. Similar leaf cells are found in a number of families of the Leucodontales and Hypnales families. The exostome in the Anomodontaceae is often yellowish, sometimes reddish at base, and structurally its peristome closely approximates that of *Leskea* Hedw.

Although the Anomodontaceae and Neckeraceae have never been considered close, there is considerable similarity between the thamnioid members of the Neckeraceae and the Anomodontaceae. Both groups have prostrate primary stems with erect secondary stems, attenuate-flagellate branch and stem tips, similar peristomes, often wavy costae, and short, rhomboidal leaf cells. The thamnioid genera generally have complanate-foliate stems, and although this is not a typical feature of the Anomodontaceae there are *Anomodon* species (*e.g.*, *A. minor*) with complanate leaves. Even the distinctive dentate leaf margins of *Herpetineuron toccoae*, an anomalous feature in the Anomodontaceae, have a close counterpart in many of the thamnioid species of the Neckeraceae.

There have been many genera placed in the Anomodontaceae since its inception, but only *Anomodon*, *Herpetineuron*, *Haplohymenium*, and *Miyabea* Broth. clearly belong there. *Thelia* Sull. *in* Sull. & Lesq. has been put there (Buck & Vitt 1986; Buck 1998), but it differs significantly from the Anomodontaceae in having more numerous, diffusely distributed rhizoidal initials, paraphyllia, and stem leaves that often have short, double costae.

1. Leaf cells smooth to bulging-mammillose; upper leaf margins dentate . . . . . 3. *Herpetineuron*
1. Leaf cells pluripapillose or bulging-mammillose; upper leaf margins entire or distantly denticulate 2

2. Leaf tips generally firm and intact, although lamina often fragile; leaf cells densely pluripapillose, papillae obscuring the cell lumina . . . . . 1. *Anomodon*
2. Leaf tips and lamina fragile, most leaf apices detached; leaf cells pluripapillose or bulging-mammillose, papillae not obscuring the cell lumina . . . . . 2. *Haplohymenium*

1. *Anomodon* Hook. & Taylor, Muscol. Brit. 79. 1818.

Plants small, medium-sized, or robust, in dull, dark green to yellow green, lax or dense mats. Primary stems creeping; leaves reduced, at times scale-like; rhizoids red brown, in clusters at abaxial side of leaf insertions, not or weakly and irregularly branched. Secondary stems erect to loosely spreading, simple or variously branched; secondary stems and branches at times transformed at tips into stolons or attenuate-flagellate branches; cross section with sclerodermis well developed, cortical cells enlarged, central strand present or absent; paraphyllia absent; pseudoparaphyllia present or absent. Secondary stem and branch leaves similar or differentiated, ovate-lanceolate, oblong-lanceolate, ligulate, or lance-ligulate from an ovate base, decurrent or non-decurrent; apices acute, broadly rounded to obtuse, at times apiculate; margins plane, erect, or recurved, entire or sparsely serrulate; costae single, ending below the apex, yellow, often wavy above, in cross section cells homogeneous, thick-walled; cells quadrate, oblate, or irregularly hexagonal, densely pluripapillose, juxtacostal cells near the insertion elongate, straight-walled or porose, weakly papillose to smooth. Dioicous. Setae elongate. Capsules erect, more or less symmetric; stomata present or absent; opercula obliquely or straight conic-rostrate; annuli rudimentary or compound; peristome double; exostome teeth white to yellow, at times reddish orange at base, narrowly triangular to linear, dorsal (outer) surface papillose-striate at base or papillose throughout, trabeculae variously projecting; endostome papillose, to 1/2 the exostome length or rudimentary, segments narrow and perforate or reduced to stubs, basal membranes low, cilia rudimentary or absent. Spores spherical, subspherical, or oblong, lightly papillose. Calyptrae cucullate, smooth.

Anomodon is a north temperate genus of 18 species (Crosby *et al.* 2000) also found in Mexico, Central America, and the Caribbean. It has creeping primary stems and long, erect, variously branched secondary stems. *Anomodon* leaves are mostly ovate at base with apices that vary from slender acuminate to broadly obtuse. Its juxtacostal leaf cells near the insertions are elongate and smooth to weakly porose, otherwise the cells are short and densely pluripapillose. The species of *Anomodon* are so similar in overall aspect that it is seems clear they represent a natural group, but they also exhibit remarkable character state variation: a stem central strand, pseudoparaphyllia, stomata, and compound annulus can be present or absent. The peristome also is variable, *e.g.*, the exostome can be white, yellowish, or faintly red, papillose throughout or horizontally striate at base, and the endostome varies from 3/4 the exostome length to rudimentary.

The leaf cell papillae in *Anomodon* are massive and often forked in a manner normally associated with Pottiaceae species. The genus, however, is closely linked to the smooth-celled *Herpetineuron.* The characteristic sinuose costa of *Herpetineuron* occurs in a weaker, flexuose to wavy state in all species of *Anomodon*, and the juxtacostal basal leaf cell differentiation of *Anomodon* is found in *H. acutifolium* (Mitt.) Granzow. Although most *Anomodon* species have papillose-crenulate leaf margins, there are some species with irregularly dentate (*A. attenuatus*) or coarsely serrate (*A. dentatus* Gao) leaf margins that approach those seen in *H. toccoae*.

Anomodon has been associated with the Leskeaceae or Thuidiaceae, since its sporophytes resemble those of the Leskeaceae and its gametophytes resemble those of the Thuidiaceae (see Granzow-de la Cerda 1997). Buck and Vitt (1986) recognized the Anomodontaceae, and moved it to the Leucodontales near the Cryphaeaceae. The positioning of the Anomodontaceae in the Leucodontales is based on the differentiation of its stems into creeping, sympodially branched primary stems with reduced leaves and erect, secondary stems with full-sized leaves. *Anomodon* shows some similarity to the thamnioid genera of the Neckeraceae in costal and leaf form, especially in those members of the genus that have more or less asymmetric, complanately arranged leaves (*e.g.*, *A. minor*). *Anomodon* was revised by Granzow-de la Cerda (1997). A revision of the east Asiatic species of *Anomodon* (Iwatsuki 1963) remains an extremely useful treatment of the genus.

The name *Anomodon* combines the Greek *a* (not), *nomo* (law or rule), and *odon* (tooth), and refers to the mistaken observation that its endostome segments came from the same cell layers as the exostome teeth.

1. Leaf apices hyaline hair-pointed; margins revolute above . . . . . 3. *A. rostratus*
1. Leaf apices broadly obtuse, rounded or acute; margins plane or revolute at base 2

2. Leaves erect-imbricate when dry; apices broadly obtuse, entire, not apiculate; costae often forked above; upper dorsal costal cells elongate, often seriate papillose; branches not stoloniform-attenuate . . . . . 2. *A. minor* var. *inaequalifolius*
2. Leaves erect-homomallous when dry; apices rounded to acute, often serrulate and apiculate; costae not or weakly branched above; upper dorsal costal cells subquadrate, smooth; branches often stoloniform-attenuate . . . . . 1. *A. attenuatus*

1. *Anomodon attenuatus* (Hedw.) Huebener, Muscol. Germ. 562. 1833. *Leskea attenuata* Hedw., Sp. Musc. Frond. 230. 1801. *Hypnum attenuatum* (Hedw.) Sm., Fl. Brit. 3: 1804, illegitimate homonym, not Dicks. *ex* With., 1801. Protologue. Ad truncos arborum inferiores in silvis humidis Germaniae.

Anomodon wrightii Müll. Hal., Hedwigia 37: 262. 1898. Protologue. Cuba ad rupes in viis cavis: Charles Wright; 1856, Musci Cubenses *Wright No. 69*.

Plants medium-sized, in dull, dark green or yellow green mats. Primary stems creeping; leaves reduced, 0.3–0.5 mm long, well spaced, scale-like to triangular, cells variously papillose to nearly smooth; rhizoids red brown, in clusters at abaxial side of leaf insertions, not or weakly and irregularly branched. Secondary stems horizontal or erect and loosely spreading, to 5 cm long, irregularly branched, secondary stems and branches often stoloniform-attenuate at the tips; cross section with sclerodermis of 2–5 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, firm- or thick-walled, central strand absent; paraphyllia and pseudoparaphyllia absent; branches usually recurved when dry. Secondary stem leaves oblong-lanceolate, to 2 mm long. Branch leaves erect and homomallous when dry, erect-spreading when wet, ovate-lanceolate from an ovate base, to 1.5 mm long, acute, apiculate, long and broadly decurrent; margins plane or erect at base, papillose-crenulate, at times sparsely serrulate at the apex, denticulate at the base of the decurrencies; costae single, ending well below the apex, yellow, wavy above, channeled on ventral surface, with quadrate, densely papillose cells on upper dorsal surface, in cross section cells homogeneous, thick-walled; upper cells quadrate, oblate, or irregularly hexagonal, 5–9 µm, densely pluripapillose by thick, branched, or C-shaped papillae, cells near the apex lightly papillose to nearly smooth, juxtacostal cells near the insertions long-rectangular, to 30 × 12 µm, porose, weakly papillose to smooth, cells in basal decurrencies enlarged, smooth to weakly papillose. Dioicous. Perigonia and perichaetia gemmate, lateral on secondary stems. Setae elongate, red to orange, flexuose, to 20 mm long. Capsules erect, 2–3 mm long, smooth, light brown; exothecial cells small, oblate, thick-walled in 3–5 rows below the mouth, becoming subquadrate and short-rectangular below; stomata at junction of urns and setae; opercula obliquely or straight conic-rostrate, to 1 mm long; annuli rudimentary, cells often clinging to capsule mouth or operculum; exostomes white to yellow above, reddish orange at base, narrowly triangular to linear, dorsal (outer) surface papillose-striate in lower half, papillose above, trabeculae laterally projecting; endostome papillose, to 3/4 the exostome length, segments narrow and perforate, basal membranes low, cilia rudimentary or absent. Spores spherical, subspherical, or oblong, lightly papillose, 9–16 µm. Calyptrae cucullate, smooth, 2–2.5 mm long.

Illustrations. Bartram (1949, Pl. 147 E–G); Nyholm (1960, Fig. 238 B); Crum and Anderson (1981, Fig. 416); Ireland (1982, Pl. 257); Crum (1983, Fig. 92 a–c); Reese (1984, Fig. 48 F–H); Sharp *et al.* (1994, Fig. 510); Granzow-de la Cerda (1997, Fig. 17 c–e); Buck (1998, Pl. 66 14–18); Nebel and Philippi (2001, p. 266). Figure 1.

Habitat. On decaying debris (twigs), tree trunks, and limestone boulders and rocks; 823–1676 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: *Standley 92104* (F, FH, NY); Baja Verapaz: *Sharp 2947* (FH, MO); Quiché: *Sharp 2429* (FH, US).

World range: Western and Eastern Canada, North-Central, Northeastern, Southwestern, South-Central, and Southeastern U.S.A.; Mexico; Central America; Caribbean; Northern, Middle, Eastern, Southwestern, and Southeastern Europe; Caucasus, Middle Asia, Siberia; Indian Subcontinent.

Dry plants of *Anomodon attenuatus* can be recognized in the field by their long, attenuate branch and secondary stem tips, recurved branches, and curved to homomallous leaves. The remarkably long-decurrent leaves of *A. attenuatus* are serrate to dentate at the margins in a manner similar to the

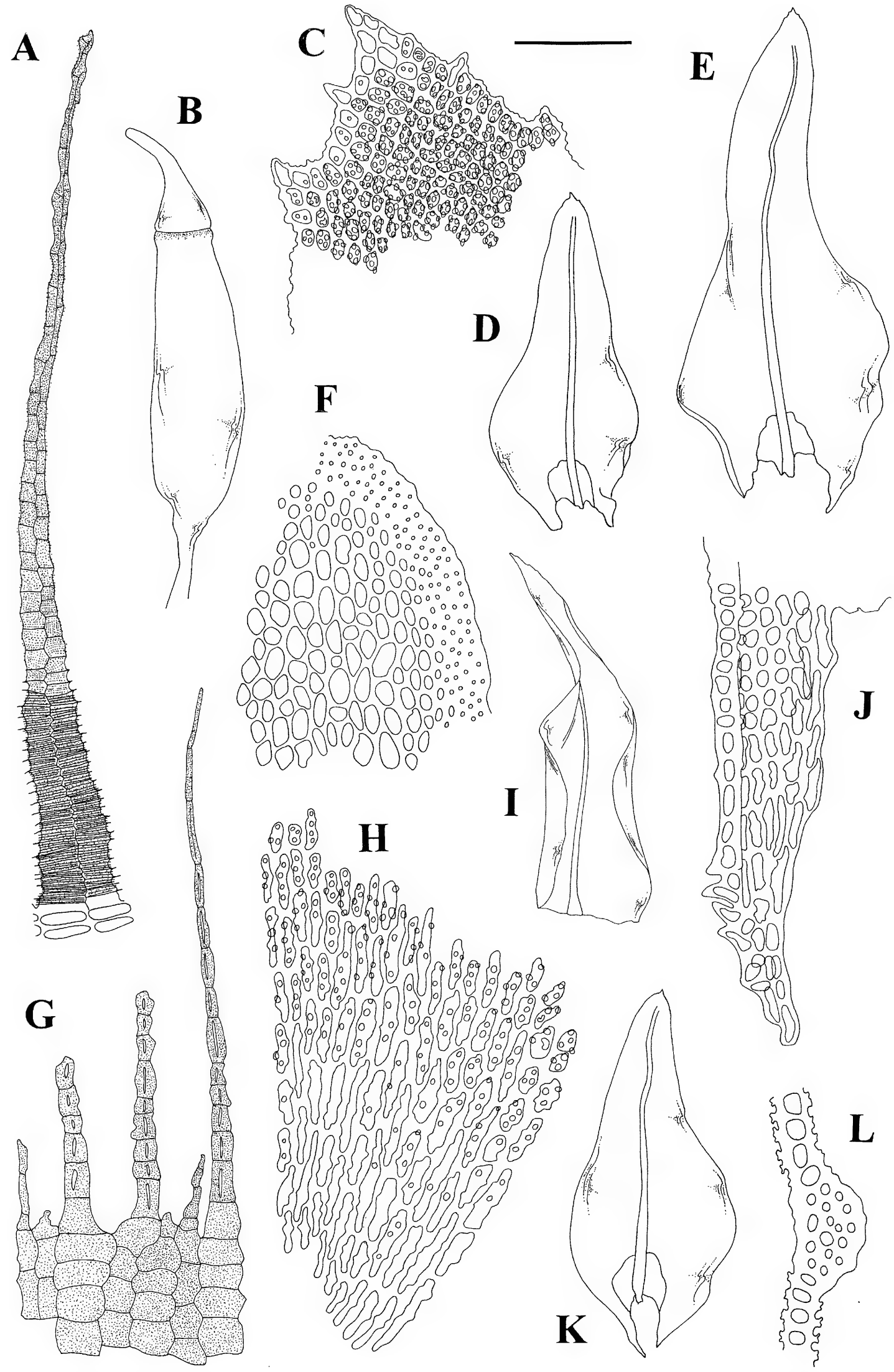
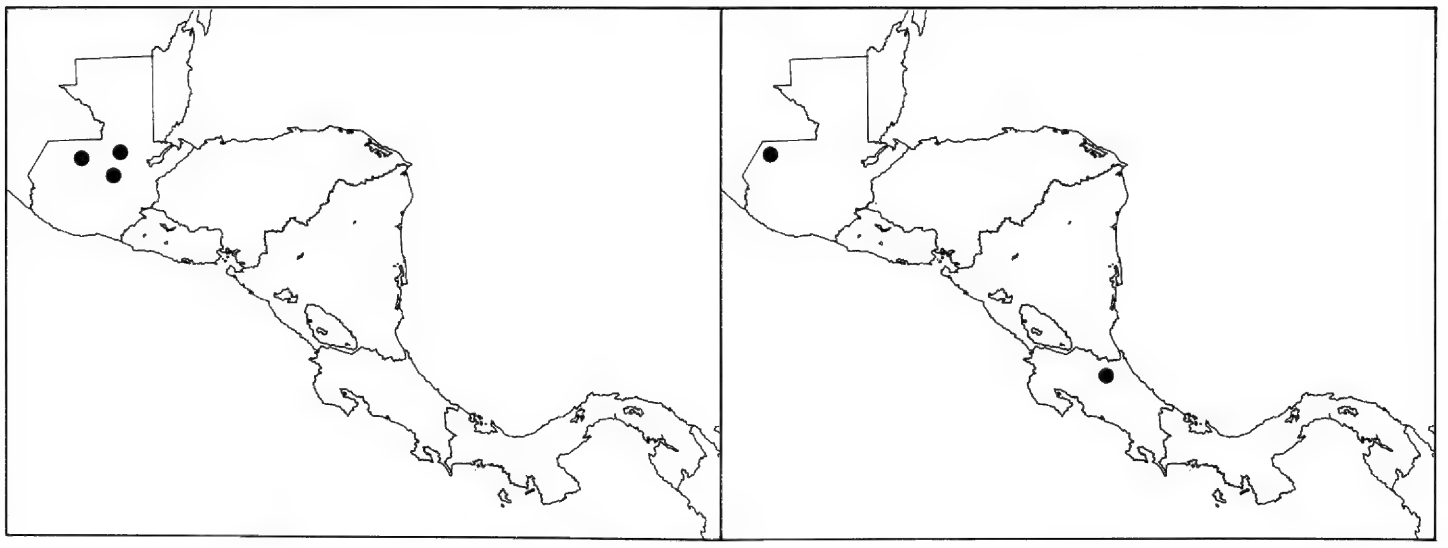


Figure 1. *Anomodon attenuatus*. A. Exostome, dorsal (outer) surface. B. Seta, capsule, and operculum. C. Leaf apex. D & K. Branch leaves. E. Secondary stem leaf. F. Stem cross section. G. Endostome, ventral (inner) surface. H. Basal leaf cells. I. Perichaetial leaf. J. Leaf decurrency. L. Cross section of costa. Scale in mm: bar = 0.05 (L); bar = 0.06 (C, H, J); bar = 0.08 (F); bar = 0.09 (A, G); bar = 0.34 (I); bar = 0.5 (D, E, K); bar = 0.9 (B). A, B, G, I from *Allen 14997*; C from *Allen 20942*; all other figure parts from *Allen 20032*.



Anomodon attenuatus *Anomodon minor* var. *inaequalifolius*

leaves found in several Orthotrichaceae genera. The leaves of *A. attenuatus* are somewhat dimorphic, with the branch leaves being entire or weakly serrulate at the apex, which is broader and more rounded than the secondary stem leaf apices. The sporophytes of *A. attenuatus* are unknown in Central America, and also rare in North America. A survey of *A. attenuatus* at MO found only seven percent with sporophytes. The exostome teeth in *A. attenuatus* are characteristically white throughout when old, but are orange to red at base when first exposed.

Anomodon rostratus differs from *A. attenuatus* in having hyaline hair-points and leaf margins that are recurved to near the apex. The leaves of *A. attenuatus* are usually apiculate and have mostly plane leaf margins, although the lower margins (especially on the branch leaves) can be erect to somewhat recurved. Although *A. minor* var. *inaequalifolius* and *A. attenuatus* both have stiffly erect, noncontorted leaves when dry, in *A. minor* var. *inaequalifolius* the leaves are erect throughout and the leaf apex is broadly rounded to rounded-obtuse, entire, and not apiculate. Granzow-de la Cerda (1997) also separated these species by the form of papillae on the upper dorsal surface. In *A. minor* var. *inaequalifolius* the upper dorsal costal cells are pellucid and have seriate papillae, while in *A. attenuatus*, especially on the branch leaves, the dorsal surface of the costa is obscured by quadrate, densely papillose cells that are similar to the laminal cells. Another good feature that distinguishes the two species is the relative development of yellowish, elongate, and porose cells that radiate from the base of the leaf. In *A. minor* var. *inaequalifolius* these cells are poorly developed and variously developed on the different sides of the costa, while those of *A. attenuatus* on both sides of the costa are exceptionally well developed.

2. *Anomodon minor* (Hedw.) Fürnr. var. ***inaequalifolius*** E. B. Bartram, Bryol. 50: 207. 1947. Protologue. Guatemala. Dept. Huehuetenango: limestone bluff, along Río Ochival, near San Miguel Acatán, alt. 5700 ft., *A. J. Sharp 4857*. Type. Dept. Huehuetenango: limestone bluff, along Río Ochival, near San Miguel Acatán, alt. 5700 ft., *A. J. Sharp 4857* (FH, holotype).

Plants small in dull, dark green mats. Primary stems creeping, irregularly branched; leaves reduced, 0.4 mm long, well spaced, scale-like, oblong-ligulate from an ovate base, wide-spreading to squarrose at tips, cells more or less smooth below, densely papillose above; rhizoids red brown, in clusters at abaxial side of leaf insertions, not or weakly and irregularly branched. Secondary stems erect-ascending, to 2 cm long, irregularly branched; cross section with sclerodermis of 2–5 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, firm- or thick-walled, central strand absent; paraphyllia and pseudoparaphyllia absent. Secondary stem leaves erect-imbricate when dry, spreading to widely spreading, complanate when wet, oblong-ligulate from an ovate base, 0.8–1.4 mm long, rounded to rounded-obtuse, not apiculate, at base one side narrow, margins broadly incurved, the other side wide, margins plane, weakly decurrent; margins papillose-crenulate; costae single, ending well below the apex, yellow, often branched above, channeled on ventral surface, upper dorsal costal cells elongate, often seriate papillose, in cross section cells homogeneous, thick-walled;

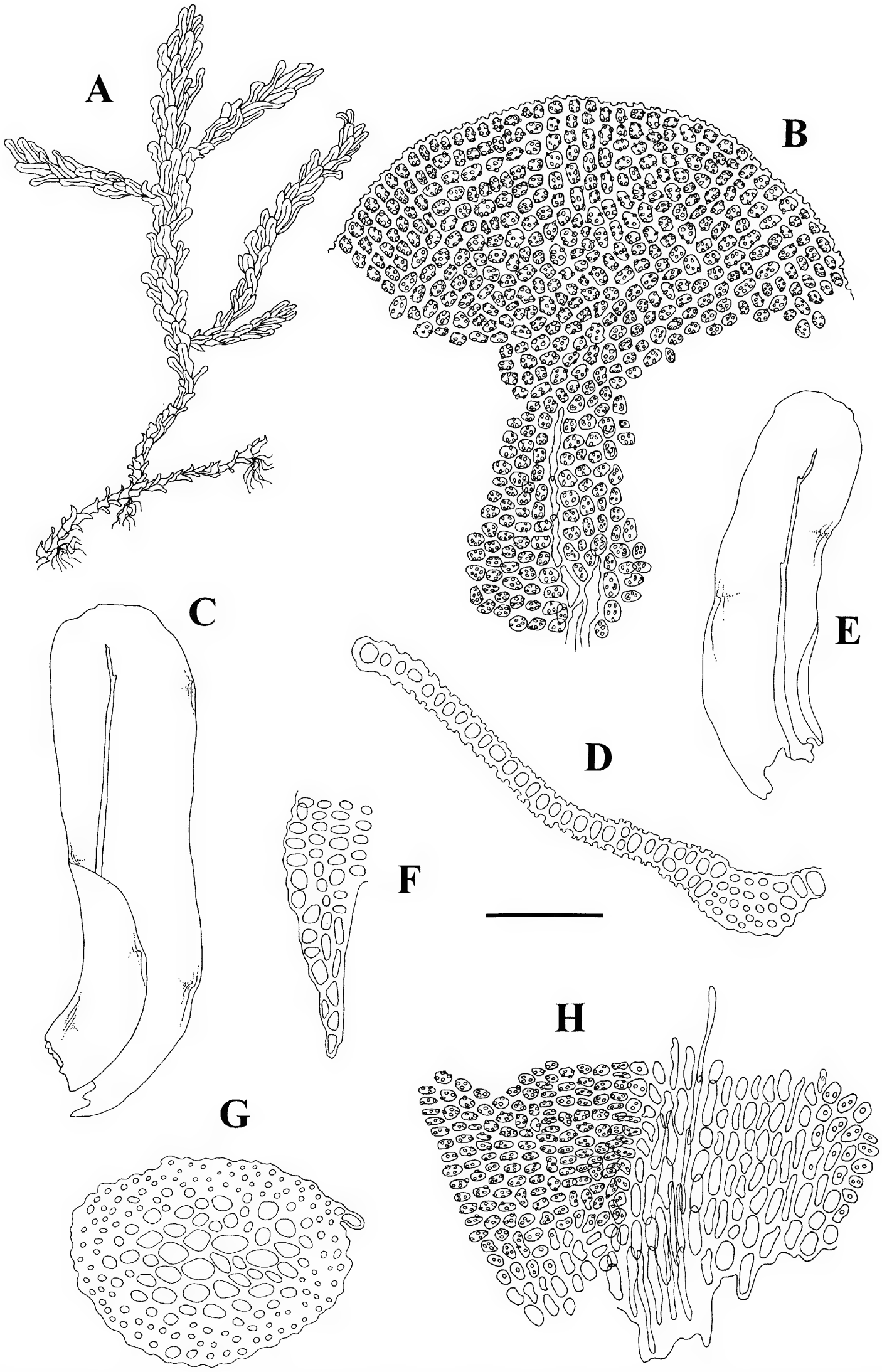


Figure 2. *Anomodon minor* var. *inaequalifolius*. A. Habit. B. Leaf apex. C & E. Leaves. D. Leaf cross section. F. Leaf decurrency. G. Stem cross section. H. Basal leaf cells. Scale in mm: bar = 0.06 (B, D, F, G, H); bar = 0.28 (C, E); bar = 1.56 (A). All figure parts from *Sharp 4857* (type).

juxtacostal cells in lower part of leaf bistratose, upper cells unistratose with occasional, scattered bistratose patches, quadrate, oblate, or irregularly hexagonal, 5–10 μm, densely pluripapillose by thick, branched, or C-shaped papillae, juxtacostal cells near the insertion on one side short-rectangular, quadrate, or oblate, 4–10 papillose, on the other long-rectangular, to 20 μm long, smooth, not porose. Dioicous. Sporophytes unknown.

Illustrations. Bartram (1949, Pl. 148 A–C). Figure 2.

Habitat. On limestone bluffs and tree bark; 1100–1737 m.

Distribution in Central America. GUATEMALA. Huehuetenango: *Sharp 4857* (FH). COSTA RICA. Heredia: *Crosby 3870A* (MO).

World range: Central America.

Anomodon minor var. *inaequalifolius* is a small species with broadly rounded, entire leaves that are erect-imbricate and not or scarcely contorted when dry. This taxon was synonymized with *A. minor* var. *minor* by Granzow-de la Cerda (1997). Although the Central American material clearly belongs within *A. minor*, it differs from the typical variety in its smaller size, more consistently equitant leaves that at base are broader on one side than the other, and most importantly in the absence of a stem central strand. As noted by Iwatsuki (1963) and Granzow-de la Cerda (1997), *A. minor* var. *inaequalifolius* is very similar to the Asian species *A. planatus* Mitt. and *A. integerrimus* Mitt. Iwatsuki (1963) treated these Asian species as *A. minor* subsp. *integerrimus*.

The hyaline hair-pointed leaves of *A. rostratus* with strongly recurved leaf margins distinguish it from *A. minor* var. *inaequalifolius*. *Anomodon attenuatus* differs from *A. minor* var. *inaequalifolius* in its larger size, curved, often stoloniform-attenuate branches, and acute, apiculate, sparsely serrulate leaves that are homomallous when dry. *Anomodon thraustus* Müll. Hal., an Asian species disjunctly present in Mexico, is similar to *A. minor* var. *inaequalifolius* in size and in having broadly rounded, entire leaves that are stiffly erect when dry. Unlike *A. minor* var. *inaequalifolius*, however, its leaf apices are fragile and often broken. In addition, its intact leaves differ from those of *A. minor* var. *inaequalifolius* in being more narrow above and in having shorter costae (2/3–3/4 the leaf length) that are completely obscured above by densely papillose laminal cells.

The aspect of *A. minor* var. *inaequalifolius* when dry is so distinctive that with experience it can be readily identified, but the species also has several features that help in its recognition. One peculiar feature is found in the basal juxtacostal cells near the leaf insertions, and may be correlated with its complanate leaves that are often infolded at the base on one side. In most leaves these cells are strongly dimorphic, with the cells on the infolded sided long-rectangular to elongate and especially thick-walled, while the cells on the other side are rectangular to subquadrate and only moderately thickened. Another distinctive feature of *A. minor* is the tendency for its leaves below the middle to be bistratose in several rows along the costa.

3. *Anomodon rostratus* (Hedw.) Schimp., Syn. Musc. Eur. 488. 1860. *Leskea rostrata* Hedw., Sp. Musc. Frond. 226. 1801. *Hypnum rostratum* (Hedw.) P. Beauv., Prodr. Aethéogam. 69. 1805. Protologue. [United States] Circa Lancaster Pensilvaniae [*Muhlenberg*].

Plants medium-sized, in dull, yellowish green, thick, dense mats. Primary stems creeping; leaves reduced, 0.6–0.7 mm long, ovate-triangular to triangular, long hair-pointed; cells pluripapillose; rhizoids red brown, in clusters at abaxial side of leaf insertions, not or weakly and irregularly branched. Secondary stems crowded, erect-ascending, 0.5–2 cm long, densely branched; cross section with sclerodermis of 2–5 rows of small, thick-walled cells, cortical cells enlarged, firm- or thick-walled, central strand well developed; paraphyllia and pseudoparaphyllia absent. Secondary stem and branch leaves erect-imbricate when dry, erect when wet, ovate-lanceolate, to 1.3 mm long, acuminate, hyaline hair-pointed, long-decurrent; margins broadly revolute above to near the apex, plane or revolute at base, papillose-crenulate, denticulate at the base of the decurrencies; costae single, ending below the apex, yellow, wavy, channeled on ventral surface, dorsal surface with elongate, seriate-papillose cells, in cross section cells homogeneous, thick-walled; upper cells hexagonal, oblong, rhomboidal to elongate, 10–24 × 3–4 μm, densely pluripapillose, papillae thick and branched, cells of the hair-point smooth; basal cells along the margins and in the alar regions oblate to quadrate, 8–10 μm, densely

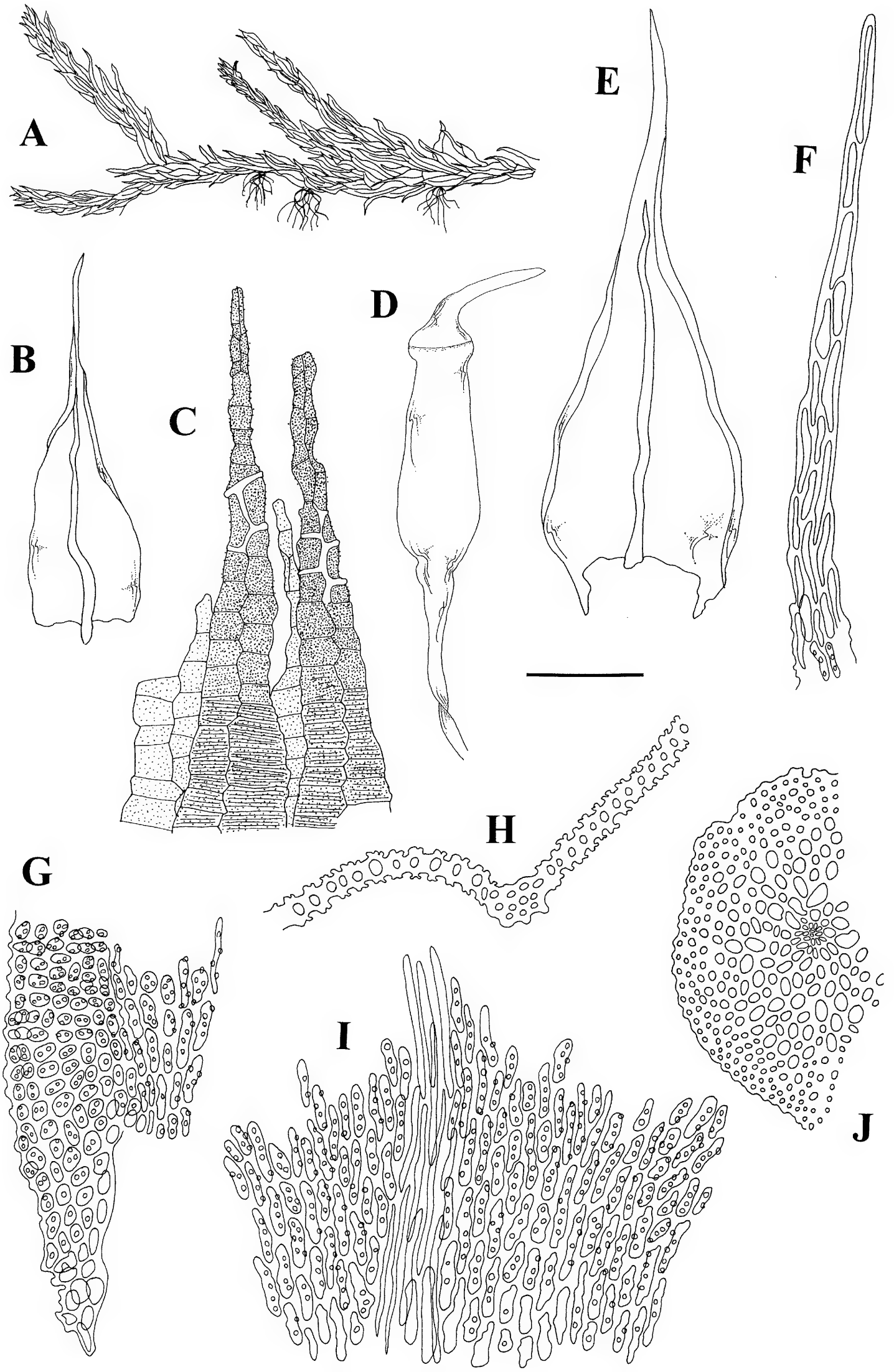
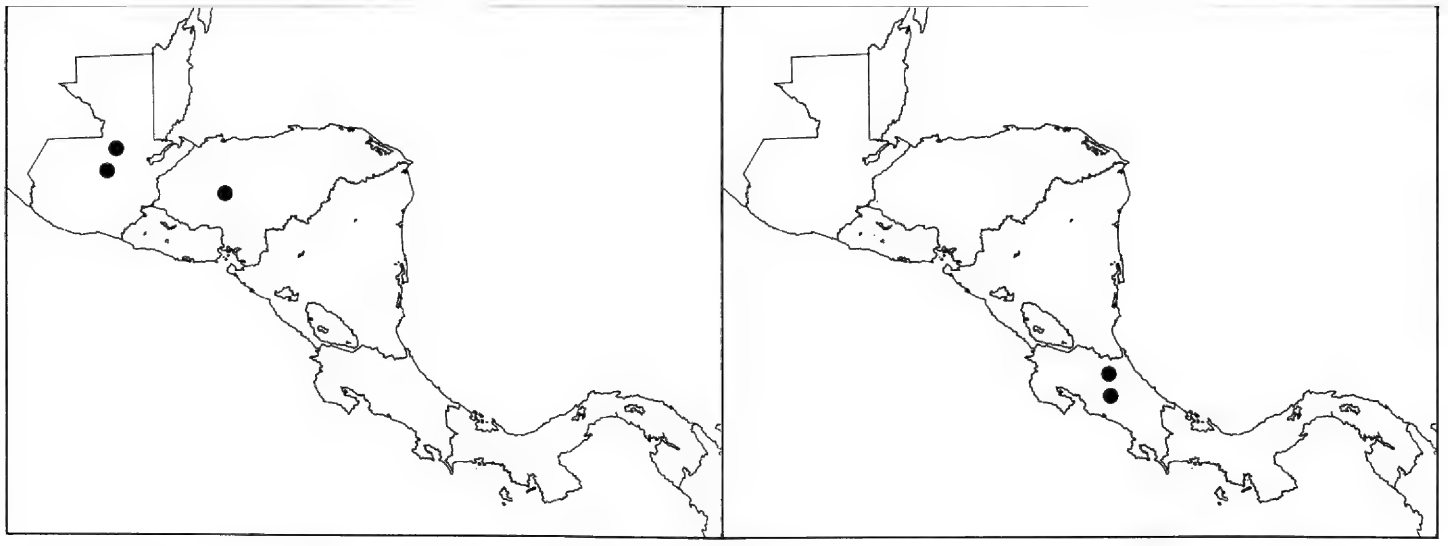


Figure 3. *Anomodon rostratus*. A. Habit. B. Branch leaf. C. Exostome, dorsal (outer) surface. D. Seta and capsule. E. Stem leaf. F. Leaf apex. G. Leaf decurrency. H. Leaf cross section. I. Basal leaf cells. J. Stem cross section. Scale in mm: bar = 0.05 (C, F, G, H, I); bar = 0.06 (J); bar = 0.28 (B, E); bar = 0.6 (D); bar = 1.56 (A). C & D from *Allen 23783*; all other figure parts from *Allen 20017*.



Anomodon rostratus *Haplohymenium triste*

pluripapillose, inner basal cells near the costa elongate, thick-walled, often porose, to 40 µm long, basal decurrency cells quadrate, weakly papillose. Dioicous. Perigonia and perichaetia gemmate, lateral on secondary stems. Setae elongate, dark red, flexuose, 7–12 mm long. Capsules erect, oval-cylindrical to elliptic, 1.0–1.5 mm long, smooth, light brown; exothecial cells small, oblate, thick-walled in 1–2 rows below the mouth, short-rectangular below; stomata at base of capsules; opercula obliquely conic-rostrate, to 1 mm long; annuli rudimentary, cells often clinging to capsule mouth or operculum; exostome white when dry, narrowly triangular, dorsal (outer) surface horizontally papillose-striate in lower half, papillose above, ventral (inner) trabeculae projecting; endostome papillose, to 3/4 the exostome length, segments narrow, rudimentary, basal membranes low, cilia absent. Spores spherical, smooth to lightly roughened, 10–15 µm. Calyptrae cucullate, smooth, 2 mm long.

Illustrations. Bartram (1949, Pl. 147 H–J); Crum and Anderson (1981, Fig. 415); Ireland (1982, Pl. 256); Crum (1983, Fig. 91); Reese (1984, Fig. 48 C–D); Sharp *et al.* (1994, Fig. 509); Granzow-de la Cerda (1997, Fig. 27); Buck (1998, Pl. 66 8–13). Figure 3.

Habitat. On limestone or calcareous boulders, vines, and tree trunks; 1360–1800 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: *Standley 90129* (F, FH); Baja Verapaz: *Sharp 2844* (FH); Quiché: *Sharp 2434* (FH). HONDURAS. Comayagua: *Centeno 193* (MO, TEFH).

World range: Western and Eastern Canada, Northwestern, North-Central, Northeastern, Southwestern, South-Central, and Southeastern U.S.A.; Mexico; Central America; Caribbean; Northern, Middle, East, Southwestern, and Southeastern Europe; Caucasus.

Anomodon rostratus often has a distinctive yellowish green color, and is immediately distinguished from the other Central American members of the genus by its long-acuminate, hyaline hair-pointed leaves. Other noteworthy features of the species include its densely matted habit, short secondary stems and branches, usually recurved upper leaf margins and inner basal leaf cells equally developed on both sides of the costa. Granzow-de la Cerda (1997) considered the endostome of *A. rostratus* well developed, but it is actually rudimentary, with the segments reaching three-quarters the length of the exostome only because of the shortness of the exostome teeth.

Central American material of *A. rostratus* differs from typical North American material of the species in having shorter, broader leaves that are often catenulate rather than erect-imbricate when dry. These plants also tend to have weakly recurved to plane leaf margins, poorly differentiated inner basal leaf cells, and short upper leaf cells. North American collections of *A. rostratus*, however, exhibit the same features on leaves from smaller, terminal branches.

Anomodon rostratus and *A. attenuatus* are placed in subgenus *Pseudoanomodon* Limpr. on the basis of their greatly branched secondary stems, acute to acuminate leaves with the inner basal leaf cells equally developed on both sides of the costa, perichaetial leaves with enlarged apical cells, rudimentary annuli, stomata present, and relatively well-developed endostome. As noted by Buck (1998),

however, they appear distantly related. *Anomodon rostratus* has a well-developed stem central strand, axillary hairs with two to three short, hyaline basal cells, small, mostly monomorphic leaves with recurved, entire upper margins, and reduced exostome teeth. In contrast, *A. attenuatus* has no stem central strand, axillary hairs with a single brown basal cell, large dimorphic stem and branch leaves with plane often distantly denticulate upper margins, and well-developed exostome teeth.

2. *Haplohymenium* Dozy & Molk., Musci Frond. Ined. Archip. Ind. 127. 1846. *Anomodon* sect. *Haplohymenium* (Dozy & Molk.) Granzow, Contr. Univ. Michigan Herb. 21: 239. 1997.

Plants small and slender, in dark green or yellow green, loose, wiry mats. Primary stems creeping, freely and irregularly branched; leaves reduced; cells smooth to weakly papillose; rhizoids red brown, in clusters at abaxial side of leaf insertions, not or weakly and irregularly branched. Secondary stems weakly differentiated, often transformed to stolons at the tips, erect and loosely spreading; cross section with sclerodermis of small, thick-walled cells, cortical cells enlarged, central strand absent; paraphyllia and pseudoparaphyllia absent. Secondary stem and branch leaves erect-imbricate when dry, spreading to squarrose when wet, ovate-lanceolate, apices acute to rounded, often apiculate, shortly decurrent, leaf lamina usually fragile, apices often detached; margins plane or erect, papillose-crenulate, at times serrulate near the apices; costae single, usually ending near midleaf (rarely 2/3 the leaf length), yellow, ventral surface somewhat channeled, with quadrate, papillose cells above, in cross section cells homogeneous, thick-walled; upper cells rounded-quadrate, subquadrate, or irregularly hexagonal, bulging-mammillose, pluripapillose, or with a single, spinose papilla, juxtacostal cells near the insertion yellow, long-rectangular, weakly papillose to smooth. Dioicous. Setae short, 2–5 mm long. Capsules globose or oblong-ovate, 0.7–1.0 mm long; stomata absent; opercula rostrate; annuli complex; exostome teeth linear, verrucose; endostome rudimentary, of a very short membrane. Calyptrae cucullate, sparsely hairy, weakly papillose.

Haplohymenium is a genus of small, delicate plants that have erect-imbricate, often fragile leaves. *Haplohymenium triste* (Ces. *ex* De Not.) Kindb., the most widespread species, has this feature especially well developed, and as a result fragile leaves are often considered of primary importance in defining the genus. Fragile leaves, however, are not consistently present within *Haplohymenium*, and since some *Anomodon* species (*e.g.*, *A. thraustus* Müll. Hal.) have extremely fragile leaves the genus has been treated as a section of *Anomodon*. This view is further supported by the remarkable amount of character state variation found in *Anomodon*. *Haplohymenium*, however, is well distinguished from *Anomodon*. The genus has a distinctive aspect due to its slender plants that have leaves erect-imbricate when dry. In addition, all species have a clear areolation even when the cells are pluripapillose because the cells are also bulging-mammillose. In contrast, the cells of *Anomodon* are densely papillose in such a way that the cells are obscured. The primary reasons for recognizing *Haplohymenium* at the generic level, however, are associated with its sporophytes. *Haplohymenium* has short setae (2–5 mm vs. 9–22 mm in *Anomodon*), short, oblong-ovate to subglobose capsules, verrucose exostome teeth, a rudimentary endostome present only as a very low membrane, and sparsely hairy calyptrae. The genus was revised by Noguchi (1957) and Granzow-de la Cerda (1997).

The name *Haplohymenium* combines the Greek *haplo* (single) with *hymen* (membrane) in reference to its much reduced endostome.

Haplohymenium triste (Ces. *ex* De Not.) Kindb., Rev. Bryol. 26: 25. 1899. *Leskea tristis* Ces. *ex* De Not., Syllab. Musc. 67. 1838. *Anomodon tristis* (Ces. *ex* De Not.) Sull. & Lesq., Musci. Bor. Ameri. 52. 1856. Protologue. [Italy] Sterilem ad terram in monte de s. Crescenzio ad Verbanum legit cl. *Cesati* v.s.

Plants small and slender, in dark green or yellow green, loose mats. Primary stems creeping, freely and irregularly branched; leaves reduced, 0.26–0.4 mm long, well spaced, triangular to slenderly acuminate from an ovate-deltoid base; cells smooth to weakly papillose; rhizoids red brown, in clusters at abaxial side of leaf insertions, not or weakly and irregularly branched. Secondary stems weakly differentiated, often transformed to stolons at the tips, erect and loosely spreading, 0.5–2.5 cm long, irregularly branched; cross section with sclerodermis of 2–3 rows of small, thick-walled cells,

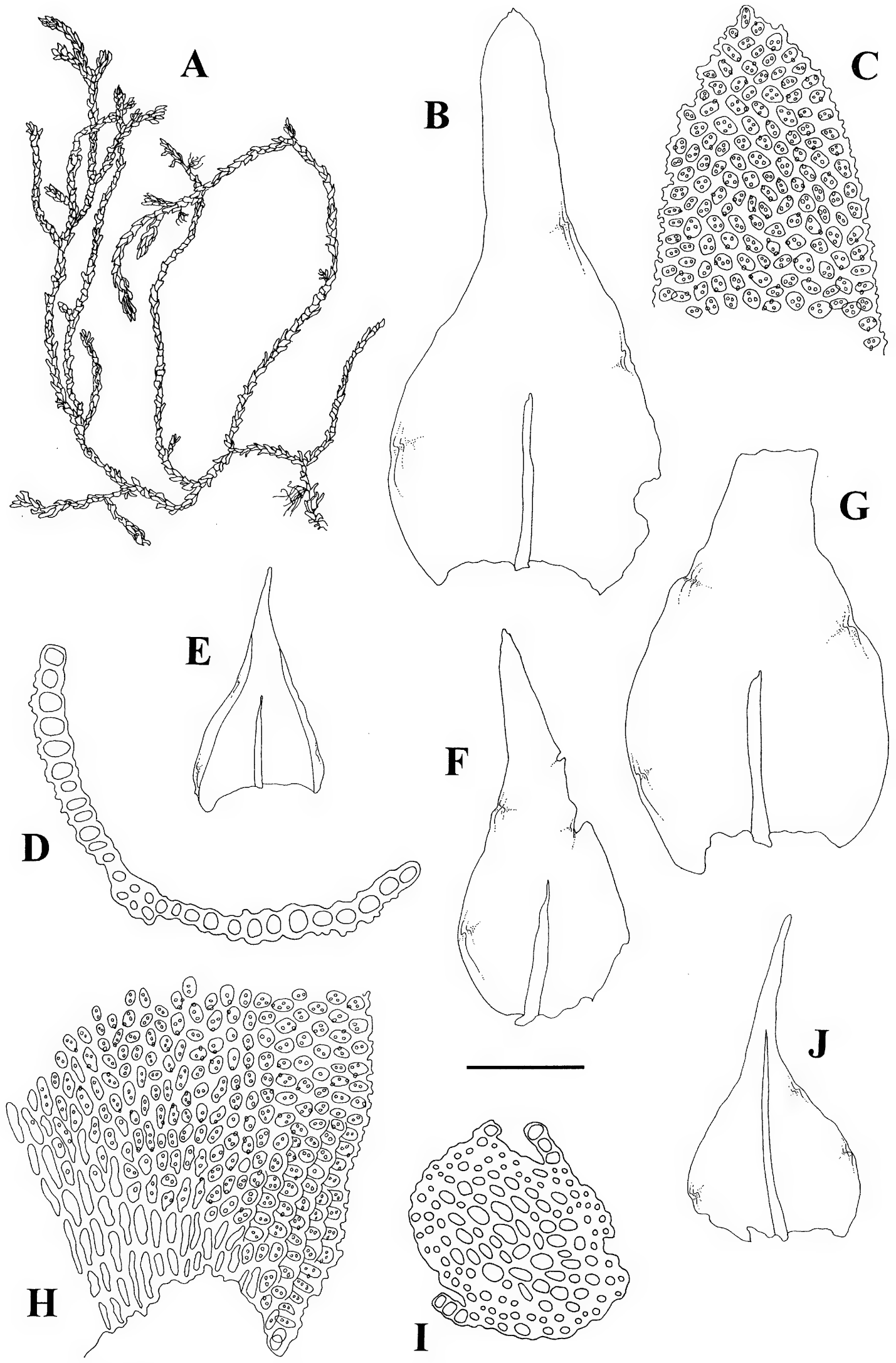


Figure 4. *Haplohymenium triste*. A. Habit. B, F & G. Secondary stem and branch leaves. C. Leaf apex. D. Leaf cross section. E & J. Primary stem leaves. H. Basal leaf cells. I. Stem in cross section. Scale in mm: bar = 0.05 (D); bar = 0.06 (C, H, I); bar = 0.13 (E, J); bar = 0.2 (B, G, F); bar = 1.56 (A). A, D, E, I, J from *Magill 11800*; all other figure parts from *Valerio 178*.

cortical cells enlarged, yellow to hyaline, firm-walled, central strand absent; paraphyllia and pseudoparaphyllia absent. Secondary stem and branch leaves erect-imbricate when dry, spreading to squarrose when wet, ovate at base, abruptly narrowed to a lanceolate or lingulate acumen, 0.5–0.9 mm long, acute to rounded, often apiculate, shortly decurrent, extremely fragile, most leaves with lamina broken and apices detached; margins plane or erect, papillose-crenulate, at times serrulate near the apex; costae single, ending at or below midleaf, yellow, ventral surface somewhat channeled, covered by quadrate, papillose cells above, in cross section cells homogeneous, thick-walled; upper cells rounded-quadrate, subquadrate, or irregularly hexagonal, 8–11 µm, bulging-mammillose and pluripapillose, juxtacostal cells near the insertions yellow, long-rectangular, 15–36 µm long, weakly papillose to smooth. Dioicous. Sporophytes not seen; known only from Asia. "Setae 3–5 mm long, more or less curved. Capsules oblong 0.8–1.2 × 0.40–0.55 mm. Operculum 0.4–0.6 mm long. Exostome teeth 0.25–0.30 mm long. Spores 20–25 µm, densely papillose. Calyptra 1.2–1.5 mm long." (Noguchi 1991).

Illustrations. Noguchi (1957, Pl. 1); Crum and Anderson (1981, Fig. 414); Ireland (1982, Pl. 255); Crum (1983, Fig. 93 a–d); Reese (1984, Fig. 48 A–B); Noguchi (1991, Fig. 364, A); Sharp *et al.* (1994, Fig. 512). Figure 4.

Habitat. On bark of tree trunks; 1800–2400 m.

Distribution in Central America. COSTA RICA. Heredia: *Crosby 9923* (MO); San José: *Valerio 178* (FH, US).

World range: Eastern Canada, North-Central, Northeastern, Southwestern, South-Central, and Southeastern U.S.A.; Mexico; Central America; Western South America; Middle and Southeastern Europe; Caucasus, Siberia, Russian Far East, China, Eastern Asia; North Central Pacific.

Haplohymenium triste has a distinctive field aspect due to its small size and occurrence in loose, wiry mats. Its leaves are erect-imbricate when dry, and this gives the branches a smooth, tightly julaceous appearance. *Haplohymenium triste* is nearly always found on the bark of tree trunks or low branches, but it sometimes occurs on granitic or limestone rocks. The leaf apices (and to a lesser degree the laminae) of *H. triste* are extremely fragile, and intact leaves normally can be found only at the tips of stems and branches. This aspect of the plants, in combination with its pluripapillose leaf cells and short, single costa distinguishes it from all other Central American mosses.

Anomodon minor var. *inaequalifolius* is somewhat similar in size to *H. triste*, and it has erect-imbricate leaves. It differs from *H. triste* in having intact leaves with broadly obtuse leaf apices and often forked costae that extend to near the leaf apex. *Anomodon thraustus*, an Asian species also found in Mexico, is similar to *H. triste* in size, and it has extremely fragile leaves with short costae that are obscured above midleaf by laminal cells. It differs from *H. triste* in having generally larger leaves (0.4–1.5 mm vs. 0.5–0.9 mm long), longer costae (2/3–3/4 the leaf vs. ending at or below midleaf), and obscure leaf areolation.

In an absolute sense *Haplohymenium* is distinguished from *Anomodon* only by features of its sporophytes and calyptrae. Even though the *H. triste* sporophyte is unknown from Central America and some *Anomodon* species have fragile laminae, the two genera are well separated since all Central American species of *Anomodon* have costae that end near the leaf apex. A more difficult feature to evaluate without previous experience with the genera is the difference in their leaf areolation. Both genera have pluripapillose leaf cells, but in *Haplohymenium* the cells are also bulging-mammillose. As result of this difference the cellular pattern in *Haplohymenium* is clear, while in *Anomodon* it is obscure.

3. *Herpetineuron* (Müll. Hal.) Cardot, Beih. Bot. Centralbl. 19(2): 127. 1905 [1906]. *Anomodon* sect. *Herpetineuron* Müll. Hal., Flora 73: 496. 1890.

Bryonorrisia L. R. Stark & W. R. Buck, Brittonia 38: 52. 1986.

Plants medium-sized, in dull, dark green or yellow green mats. Primary stems creeping with irregularly spaced, erect secondary stems or primary stems turning upward and becoming erect with primary stems continuing from lateral buds; leaves reduced, well spaced; cells smooth; rhizoids red brown, in clusters at abaxial side of leaf insertions, not or weakly and irregularly branched. Secondary stems erect, curved when dry, at times transformed to stolons at the tips, sparsely and irregularly

branched, at times with slender, flagellate branches; cross section with sclerodermis present, cortical cells enlarged, firm-walled, central strand well developed; paraphyllia absent; pseudoparaphyllia absent. Secondary stem and branch leaves erect-flexuose, subtubulose when dry, erect-spreading from the insertions when wet, ovate-lanceolate, acute to short-acuminate, not or variously decurrent; margins plane above, narrowly recurved at base, serrate or coarsely serrate by uni- or multicellular teeth above; costae single, subpercurrent to percurrent, straight or flexuose above, not channeled on ventral surface, in cross section cells homogeneous, thick-walled, enlarged, at times guide cells weakly differentiated; upper cells rhombic to subquadrate, or oblate, smooth, bulging-mammillose or prorate, firm-walled, juxtacostal cells near the insertion weakly differentiated; alar cells oblate. Dioicous. Perichaetia and perigonia gemmate, lateral on secondary stems. Setae elongate. Capsules erect, symmetric, cylindrical to elliptic; exothecial cells small, oblate, thick-walled at mouth; stomata present; opercula conic; annuli of enlarged, thick-walled cells; exostome teeth narrowly triangular, weakly cross-striate at base, papillose above; endostome to 1/2 the exostome length, segments narrow and perforate, cilia absent. Spores papillose. Calyptrae cucullate, naked, smooth.

Herpetineuron is a genus of two species, *H. toccoae* and *H. acutifolium* (Mitt.) Granzow, found principally in the Northern Hemisphere. The genus has creeping primary stems and sparsely branched, often attenuate secondary stems that are curved to circinate when dry. Its leaves are ovate-lanceolate, gradually narrowed to the apex, and they have smooth to bulging-mammillose oblate cells at the basal angles, but otherwise more or less rhomboidal cells throughout. Its costae are single, strong, yellow, and variously curved to sinuose above. *Herpetineuron* has elongate setae, erect capsules, narrow exostome teeth that are variously striate-papillose on the lower dorsal surface, and reduced endostomes. The genus is remarkably close to *Anomodon*, and indeed only the presence of smooth to bulging-mammillose leaf cells in *Herpetineuron* clearly separate the two genera.

Enroth (1991a) supported the placement of *H. acutifolium* in the genus *Bryonorrisia* because of its clustered branching pattern, unicellular marginal teeth, narrower, less sinuose costae, non-mammillose leaf cells, more highly differentiated basal juxtacostal cells, weakly developed stem central strands, and better developed peristomes. This position was also followed by Buck and Goffinet (2000) and Goffinet and Buck (2004). However, when considering these differences in the context of character variation within the Anomodontaceae (especially *Anomodon*) they appear more important at the species rather than generic level.

The name *Herpetineuron* combines the Greek *herpeton* (snake) with *neuron* (nerve), and it refers to the strongly sinuose costa of *H. toccoae*.

Herpetineuron toccoae (Sull.) Cardot, Beih. Bot. Centralbl. 19(2): 127. 1905 [1906]. *Anomodon toccoae* Sull. & Lesq. *ex* Sull. *in* A. Gray, Manual (ed. 2) 658. 1856. *Thamnium toccoae* (Sull.) Kindb., Canad. Rec. Sci. 6: 19. 1894. Protologue. [United States] Ad rupes, prope Toccoa Falls Georgiae superioris, sterilis. Sull. & Lesq. *Musci Bor.-Amer. 240.* Type. Hab. ad rupes, prope *Toccoa Falls* Georgiae superioris, sterilis, *Musci Bor.-Amer. 240* (MO, isotype; an isotype packet at US contains no plants of this species).

Plants medium-sized, in dull, dark green or yellow green mats. Primary stems creeping, to 5 cm long, with irregularly spaced, erect secondary stems or primary stems turning upward and becoming erect with primary stems continuing from lateral buds; leaves reduced, 1.0–1.2 mm long, well spaced, spreading from insertion when wet, deltoid to triangular-ovate, acuminate; margins entire to distantly serrulate, plane or narrowly recurved at base; cells smooth; rhizoids red brown, in clusters at abaxial side of leaf insertions, not or weakly and irregularly branched. Secondary stems erect or at times transformed to stolons at the tips, curved when dry, to 3.5 cm long, sparsely and irregularly branched, at times with slender, flagellate branches; cross section with sclerodermis of 3–5 rows of small, thick-walled cells, cortical cells enlarged, yellow to hyaline, firm-walled, central strand well developed; paraphyllia absent; pseudoparaphyllia absent. Secondary stem and branch leaves erect-flexuose, subtubulose when dry, erect-spreading from the insertions when wet, ovate-lanceolate, at times slightly falcate, 1.5–2.5 mm long, acute to short-acuminate, more or less plicate at base, not or weakly decurrent; margins plane above, narrowly recurved at base, coarsely serrate above by multicellular teeth; costae single, subpercurrent to percurrent, flexuose above, not channeled on ventral surface, in cross section cells homogeneous, thick-walled, at times guide cells weakly differentiated; upper cells rhombic to sub-

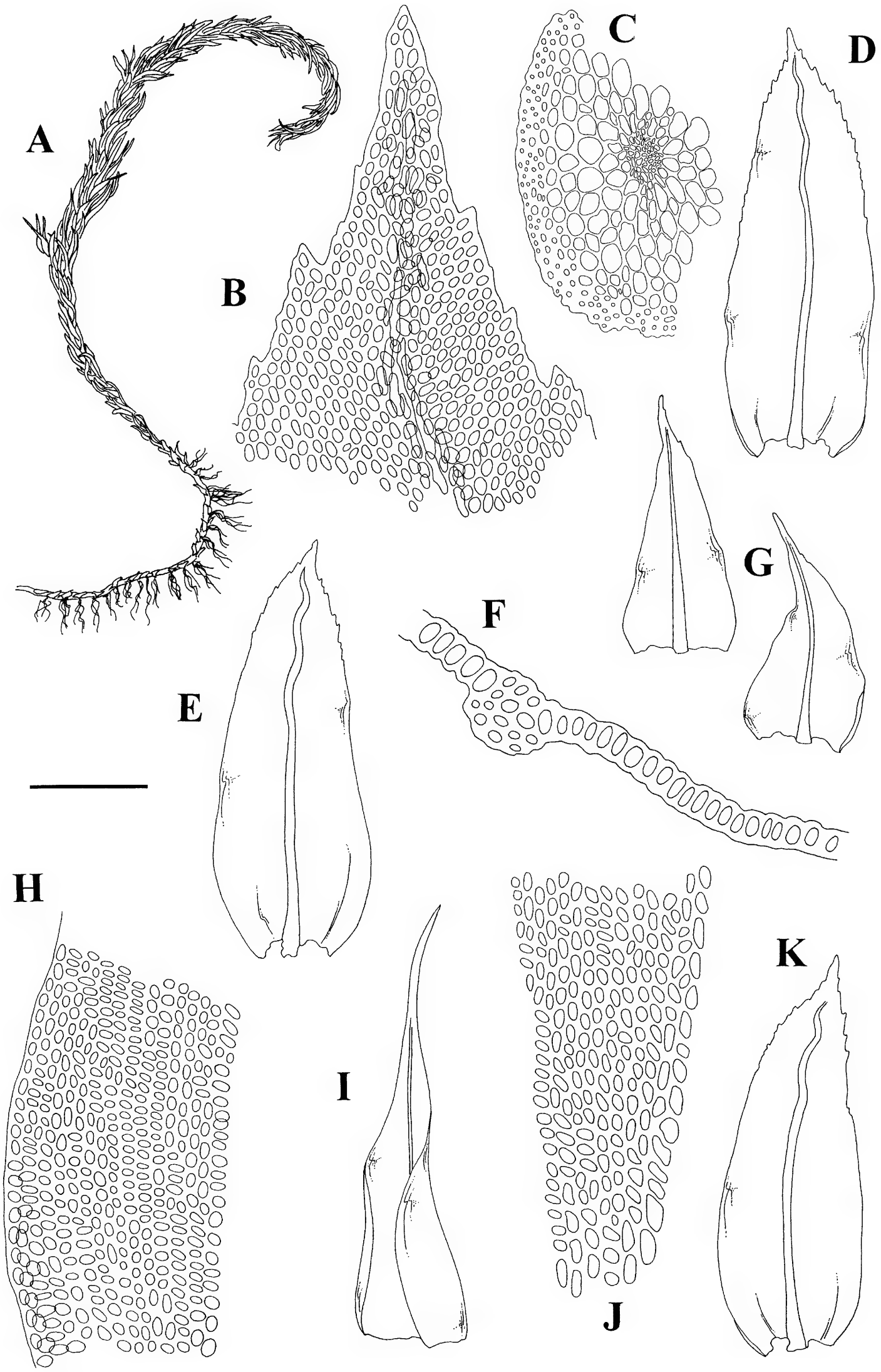
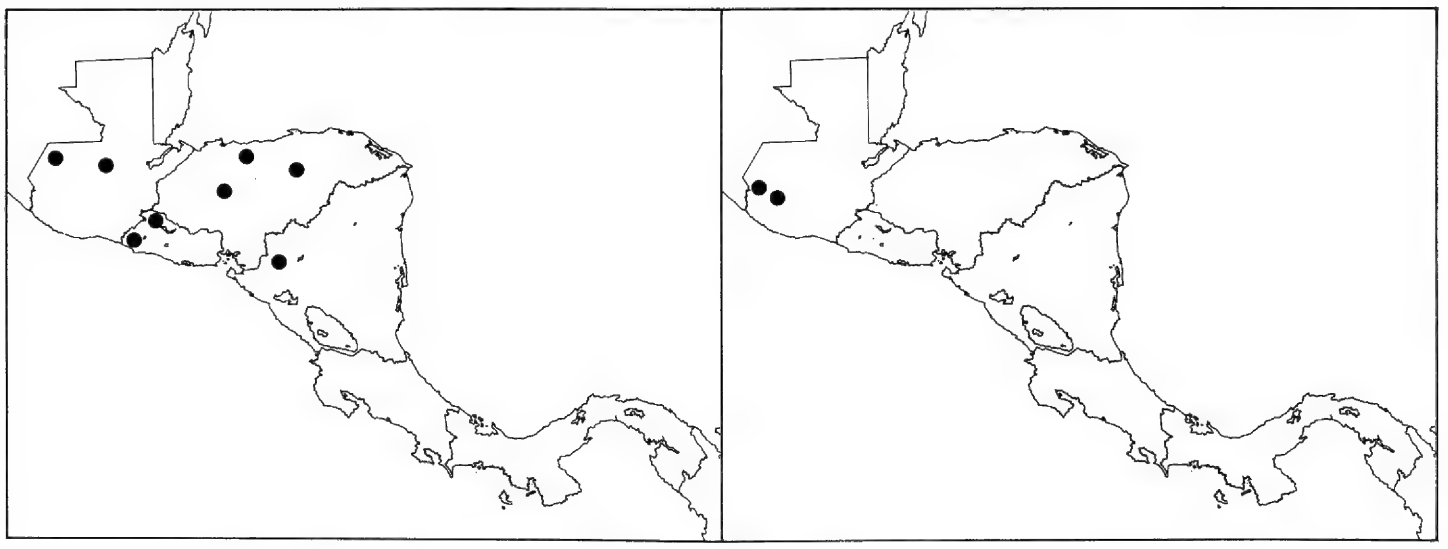


Figure 5. *Herpetineuron toccoae*. A. Habit. B. Leaf apex. C. Stem in cross section. D, E & K. Leaves. F. Leaf cross section. G. Primary stem leaves. H. Basal leaf cells. I. Perichaetial leaf. J. Median leaf cells. Scale in mm: bar = 0.06 (B, F, H, J); bar = 0.08 (C); bar = 0.5 (D, E, G, I, K); bar = 4.3 (A). All figure parts from *Olson 83-8*.



Herpetineuron toccoae *Braunia andrieuxii*

quadrate, or oblate, 6–8 µm, smooth or bulging-mammillose, firm-walled, juxtacostal cells near the insertions weakly differentiated, oblong to elongate, 10–20 µm long; alar cells oblate. Dioicous. Perichaetia gemmate, lateral on secondary stems, 2–3 mm long; inner perichaetial leaves oblong-lanceolate, long, slenderly acuminate to setaceous, margins entire to obscurely serrulate; costae ending in the acumina; upper cells oblong-elongate; paraphyses present. Sporophytes and perigonia not known from Central America, description from Granzow-de la Cerda (1997) and Buck (1998). Setae elongate, orange to reddish brown, flexuose, 9–16 mm long. Capsules erect, symmetric, 2–3 mm long, yellow to reddish brown; exothecial cells small, oblate, thick-walled in 3–5 rows below the mouth, becoming short-rectangular below; stomata present; opercula high-conic, to 1 mm long; annuli of 1–2 rows of enlarged, thick-walled cells; exostome white to yellow, narrowly triangular, dorsal (outer) surface weakly cross-striate at base, papillose above; endostome papillose, to 1/2 the exostome length, segments narrow, perforate, basal membrane 0.05–0.15 mm high, cilia absent. Spores papillose, 11–22 µm. Calyptrae cucullate, naked, smooth.

Illustrations. Grout (1934, Pl. 56 A); Bartram (1949, Pl. 149 A–C); Breen (1963, Pl. 96 5–7); Crum and Anderson (1981, Fig. 420); Reese (1984, Fig. 48 I–K); Noguchi (1991, Fig. 369 B); Sharp *et al.* (1994, Fig. 513 A–C); Buck (1998, Pl. 66 1–7). Figure 5.

Habitat. On vertical rock faces, soil over rocks, and on bark of trees; 110–1600 m.

Distribution in Central America. GUATEMALA. Baja Verapaz: *Sharp 2650* (TENN); Huehuetenango: *Standley 81215* (F). EL SALVADOR. Ahuachapán: *Winkler* 608 (TUB, Winkler 1965); Chalatenango: *Winkler* 607 (TUB, Winkler 1965). HONDURAS. Atlántida: *Allen 17227* (MO, TEFH); Comayagua: *Allen 13403* (MO); Olancho: *Olson 83-8* (MO). NICARAGUA. Estelí: *Stevens 11754* (MO, HNMN).

World range: North-Central, Southwestern, South-Central, and Southeastern U.S.A.; Mexico; Central America; Caribbean; Western and Southern South America, Brazil; West, Northeast, West-Central, East, and South Tropical Africa, Southern Africa, Western Indian Ocean; Siberia, Russian Far East, Mongolia, China, Eastern Asia; Indian Subcontinent, Indo-China, Malesia; Australasia; Southwestern Pacific.

Herpetineuron toccoae usually is dark green in color and often forms dense mats. When dry its plants can be recognized in the field by their curved to circinate secondary stems and branches that have erect-flexuose, subtubular leaves. Important microscopic leaf features of the species include its margins that are coarsely dentate by mulitcellular teeth, and firm-walled, usually bulging-mammillose, mostly rhomboidal leaf cells. Perhaps the most distinctive and characteristic leaf feature of *H. toccoae* is its yellow, remarkably sinuose costa.

Herpetineuron acutifolium occurs nearby in Mexico. It differs from *H. toccoae* in having distinctly decurrent leaves with unicellular marginal teeth, less wavy costae, non-mammillose leaf cells, more highly differentiated basal juxtacostal cells, and weakly developed stem central strands.

HEDWIGIACEAE

Hedwigiaceae Schimp., Coroll. Bryol. Eur. 52. 1856.

Plants small, medium-sized or robust, in tufts or mats. Primary stems creeping; leaves reduced, often widely spaced; rhizoids red brown, in moderate-sized clusters at abaxial side of leaf insertions, not or weakly and irregularly branched. Secondary stems erect, erect-ascending, or loosely spreading, variously branched, at times stoloniferous at tips or with flagelliform branches; cross section with sclerodermis present, cortical cells enlarged, firm-walled, central strand absent; paraphyllia and pseudoparaphyllia absent. Secondary stem leaves and branch leaves variously decurrent; apices acuminate or acute; basal margins plane, erect, or recurved, upper margins plane or incurved; costa absent; upper cells quadrate, short-rectangular or rectangular, thick-walled, at times sinuose, pluripapillose; basal median cells long-rectangular, thick-walled, porose, pluripapillose; alar cells short-rectangular, quadrate to oblate, thick-walled, smooth or papillose. Autoicous or paroicous. Perigonia gemmate, sessile on secondary stems and branches. Perichaetia terminal, perichaetial leaves erect, elongate, overtopping the capsules, margins entire or with long, hyaline, pluripapillose cilia. Setae short or elongate. Capsules exserted or immersed, erect, globose, subglobose, cupulate, broadly oblong, or cylindrical-elliptic; exothecial cells small below the mouth, lower cells enlarged, neck cells small; stomata phaneroporic or cryptoporic in neck; opercula obliquely conic-rostrate or plano-convex to umbonate; annuli rudimentary; peristome absent, at times the deoperculate capsule mouth closed by a membrane; isosporous or anisosporous. Spores massive, undergoing endosporic germination, becoming multicellular before dispersal. Calyptrae mitrate-cucullate, conic-cucullate, or conic-mitrate, smooth, sparsely or densely hairy.

The Hedwigiaceae consist of four, very similar genera: two with exserted capsules (*Braunia* Bruch & Schimp. *in* B.S.G., *Pseudobraunia* (Lesq. & James) Broth.), and two with immersed ones (*Hedwigia* P. Beauv., *Hedwigidium* Bruch & Schimp. *in* B.S.G.). The gametophytes of *Hedwigia* and *Pseudobraunia* are so similar they are sometimes considered synonymous (De Luna 1992) despite their different setae lengths. *Hedwigia* and *Hedwigidium* have also been synonymized (Nyholm 1960; Scott & Stone 1976; Smith 1978; Casas 1991; Hedenäs 1998; Cortini Pedrotii 2001; Smith 2004). *Braunia*, with 23 species (Crosby *et al.* 2000), is by far the largest genus. That genus, however, exhibits such great gametophytic variation that if setae length is disregarded one might consider merging all four genera.

The Hedwigiaceae genera share a remarkable number of features. The family is acrocarpous (De Luna 1992), but occurs in tufts or mats due to a combination of sympodial and adventitious branching. All members of the family have unbranched or rarely branched rhizoids that occur in clusters at the abaxial side of the leaf insertions. The stems of the Hedwigiaceae lack central strands, paraphyllia, and pseudoparaphyllia. All members of the family have ecostate, more or less oval to oblong leaves. Leaf areolation is a strong unifying feature of the family. The leaf cells are thick-walled throughout, often sinuose, and densely papillose. They are short above, elongate-rectangular in the basal median regions, and oblate, quadrate, or short-rectangular in the alar regions. All members of the family have eperistomate capsules, and globular protonemata development (De Luna 1990).

The Hedwigiaceae are usually placed near the Leucodontaceae (Brotherus 1925; Crum & Anderson 1981; Vitt 1984; Crum 1994a) or Orthotrichaceae (Nyholm 1960; Smith 1978; Walther 1983; De Luna 1995; Hedenäs 1998; Buck & Goffinet 2000). However, the presence of sympodially branched, acrocarpous stems in the genus *Schoenobryum* Dozy & Molk. may indicate a relationship of the family to the Cryphaeaceae. The presence of acrocarpous stems in the Orthotrichaceae is also a primary reason for placing the Hedwigiaceae near that family. Evidence for a relationship between the Hedwigiaceae and Leucodontaceae is present in a number of features: rhizoidal form and rhizoidal initial position, ecostate leaves, and a distinctive leaf cell areolation in which the cells are thick-walled throughout, short above, elongate-rectangular in the basal median regions, and oblate, quadrate, or short-rectangular in the alar regions. Both families also have some species with endosporically germinated protonemata.

1. Leaf apices hyaline and broad; cells with high, stout, often forked papillae; secondary stems and branches rarely stoloniferous; stomata cryptoporic . . . . . 2. *Hedwigia*
1. Leaf apices concolorous, or narrow with capillary hyaline tips; cells with low, simple, papillae; secondary stems and branches often stoloniferous; stomata phaneroporic 2

2. Capsules immersed; leaf alar region red to orange. . . . . 3. *Hedwigidium*
2. Capsules exserted; leaf alar region yellow . . . . . 1. *Braunia*

1. *Braunia* Bruch & Schimp. *in* B.S.G., Bryol. Eur. 3: 159. 1846 (fasc. 29–30).

Plants medium-sized, in yellow green mats. Primary stems creeping, irregularly branched; leaves reduced, well spaced, scale-like; rhizoids red brown, in sparse clusters at abaxial side of leaf insertions, not or rarely branched. Secondary stems horizontal or erect and loosely spreading, irregularly branched, often with lateral stolons or transformed to stolons at the tips; cross section with sclerodermis and firm-walled cortex, central strand absent; paraphyllia and pseudoparaphyllia absent. Secondary stem and branch leaves oblong-ovate, erect-imbricate or spreading to squarrose above when dry, spreading to wide-spreading when wet, variously plicate, acuminate and concolorous or ending in a slender, hyaline hair-point, shortly decurrent; margins narrowly recurved throughout or in the lower 1/2 or less, often erose at the apex; costa absent; upper cells short-rectangular to rectangular, thick-walled, not or strongly sinuose, pluripapillose; basal median cells long-rectangular, thick-walled, porose, pluripapillose; alar cells short-rectangular, quadrate, or oblate, thick-walled, smooth. Autoicous or paroicous. Perichaetial leaves erect, elongate. Setae elongate. Capsules erect, cylindrical-elliptic or globose to subglobose; exothecial cells small below the mouth, lower cells enlarged, neck cells small; stomata phaneroporic, in neck; opercula obliquely conic-rostrate; annuli rudimentary, cells often clinging to capsule mouth or operculum; peristome absent, at times the mouth closed by a membrane; isosporous or anisosporous. Spores massive, undergoing endosporic germination and becoming multicellular before dispersal. Calyptrae mitrate-cucullate, smooth or sparsely hairy.

Braunia is a genus of 23 (Crosby *et al.* 2000) mostly Southern Hemispheric species. Although De Luna (1992) recognized only 16 species of *Braunia*, no synonymy was included with his species list. The genus is distinguished from other Central American Hedwigiaceae genera by its long setae; *Hedwigia* and *Hedwigidium* have immersed capsules. The leaves of *Hedwigia* are also distinguished from those of *Braunia* in having very broad, hyaline hair-points and cells with high, often branched papillae. *Hedwigidium*, on the other hand, is gametophytically so close to *Braunia* that collections without sporophytes are almost impossible to place to genus.

The name *Braunia* commemorates Alexander Carl Heinrich Braun (10 May 1805–29 March 1877), Professor and Director of the Berlin Botanical Garden (Frahm & Eggers 2001). *Braunia* Bruch & Schimp. is an illegitimate later homonym of *Braunia* Hornsch., but the name in the sense used here has been conserved (McNeill *et al.* 2006).

1. Leaf apices spreading when dry, hyaline, capillary hair-pointed; setae 3–5 mm long; capsules subglobose . . . . . 3. *B. squarrulosa*
1. Leaf apices erect-imbricate when dry, concolorous, acuminate; setae 7–20 mm long; capsules ellipsoid-cylindrical 2

2. Leaf margins recurved at base, plane above midleaf; upper median cells not or weakly sinuose; plants autoicous. . . . . 1. *B. andrieuxii*
2. Leaf margins recurved to near the apex; upper median cells strongly sinuose; plants paroicous. . . . . 2. *B. secunda*

1. *Braunia andrieuxii* Lorentz, Moosstudien 164. 1864. *Braunia secunda* (Hook.) Schimp. var. *andrieuxii* (Lorentz) Thér., Smithsonian Misc. Collect. 78(2): 24. 1926. Protologue. Mexico, in monte St. Felipe prope Oaxacam leg. *Andrieux*.

Plants medium-sized, in yellow green or reddish yellow mats. Primary stems creeping, irregularly branched; leaves well spaced, reduced, ovate, abruptly acuminate, erect below, squarrose-recurved

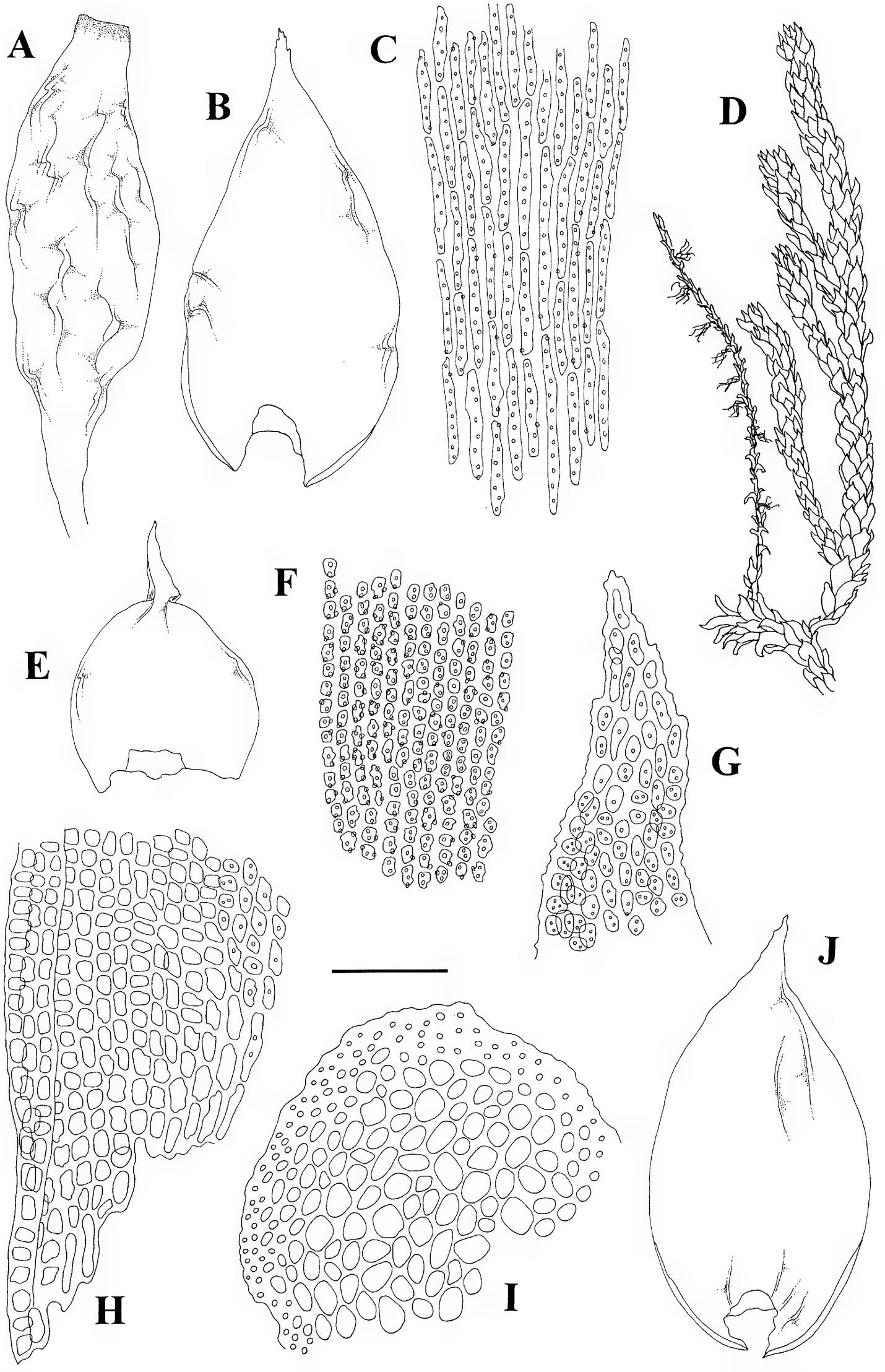
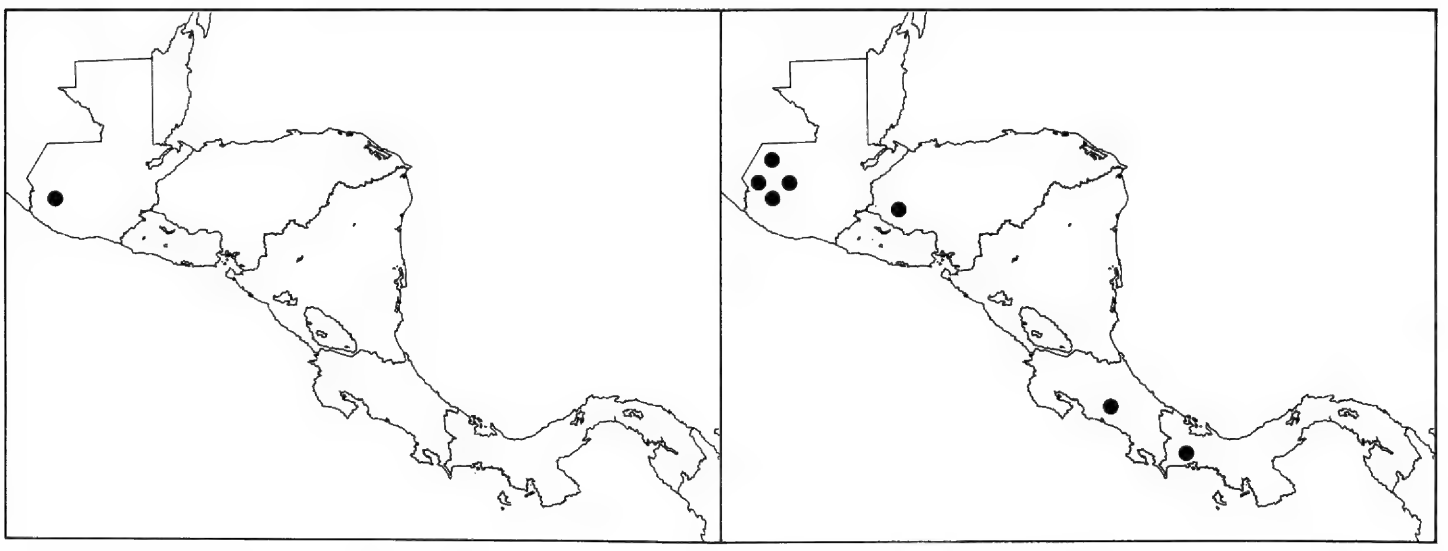


Figure 6. *Braunia andrieuxii*. A. Seta and capsule. B & J. Leaves. C. Basal leaf cells. D. Habit. E. Stipe leaf. F. Upper leaf cells. G. Leaf apex. H. Leaf alar region. I. Stem in cross section. Scale in mm: bar = 0.06 (C, F, G, H); bar = 0.08 (I); bar = 0.26 (E); bar = 0.5 (B, J); bar = 0.6 (A); bar = 3.3 (D). A from *Nesom & Wells 53*; all other figure parts from *Standley 83237*.



Braunia secunda *Braunia squarrulosa*

above, 0.5–0.6 mm long; cells pluripapillose; rhizoids red brown, in sparse clusters at abaxial side of leaf insertions, not or rarely branched. Secondary stems horizontal and often transformed to stolons at the tips or erect and loosely spreading, 3–5 cm long, irregularly branched, branches often transformed to stolons at the tips; cross section with sclerodermis of 2–5 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, firm- or thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent. Secondary stem and branch leaves erect-imbricate when dry, wide-spreading when wet, oblong-ovate, obscurely plicate, 1.5–2 mm long, shortly acuminate, shortly decurrent; margins plane above, narrowly recurved in lower 1/2 or less, apices sparsely serrulate to erose; costa absent; upper cells quadrate to short-rectangular, 10–14 µm, thick-walled, weakly sinuose, pluripapillose; basal median cells long-rectangular, to 70 × 4 µm, thick-walled, porose, pluripapillose; alar cells short-rectangular, quadrate, or oblate, 6–12 µm long, thick-walled, smooth. Autoicous. Perichaetial leaves erect, elongate. Setae elongate, yellow, becoming red to orange with age, 7–20 mm long. Capsules erect, cylindrical to elliptic, 2 mm long, wrinkled to irregularly furrowed when dry, light brown, narrowed at the mouth, at times strongly constricted at neck; exothecial cells small, red, thick-walled in 10–15 rows below the mouth, becoming lax, irregularly quadrate to short-rectangular below, neck cells small, irregularly subquadrate to short-rectangular; stomata in neck; opercula obliquely conic-rostrate, to 1 mm long; annuli rudimentary, cells often clinging to capsule mouth or operculum; peristome absent. Spores irregularly subspherical to oblong, papillose, 18–26 µm. Calyptrae cucullate, smooth, 3.5–4.5 mm long.

Illustrations. Bartram (1949, Pl. 106 D–F, as *B. secunda*); Sharp *et al.* (1994, Fig. 497 a–f, as *B. secunda*). Figure 6.

Habitat. On rocks; 2280–2400 m.

Distribution in Central America. GUATEMALA. Quetzaltenango: *Standley 83237* (F, FH, NY); San Marcos: *Croat 41046* (MO).

World range: Southwestern and South-Central U.S.A.; Mexico; Central America.

Braunia andrieuxii is often considered a variety (Thériot 1926) or synonym (Sharp *et al.* 1994) of *B. secunda*, because they have similar leaf shapes and cylindrical-elliptic capsules that are constricted at the mouth. De Luna (1992) recognized *B. andrieuxii* at the species level. *Braunia secunda* leaves differ from those of *B. andrieuxii* in having longer, narrower apices, margins recurved to near the apex, and longer, strongly sinuose upper leaf cells. The marginal and leaf apex difference between the two species is so distinctive that many times collections can be separated with a dissecting microscope. *Braunia squarrulosa* is usually distinguished from *B. andrieuxii* by its hair-pointed leaves; however, both species have similarly shaped leaves with margins recurved only in the lower half or less, and some collections of *B. squarrulosa* have weakly hair-pointed leaves. All collections of *B. squarrulosa* differ from *B. andrieuxii* in having strongly sinuose upper leaf cells. In contrast, the upper leaf cells in *B. andrieuxii* are straight-walled or weakly sinuose.

2. *Braunia secunda* (Hook.) Bruch & Schimp. *in* B.S.G., Bryol. Eur. 3: 161. 1846 (fasc. 29–30). *Hedwigia secunda* Hook., Musci Exot. 1: 46. 1818. *Anoectangium secundum* (Hook.) Steud., Nomencl. Bot. 2: 59. 1824. *Harrisonia secunda* (Hook.) Spreng., Syst. Veg. 4(1): 145. 1827. *Neckera secunda* (Hook.) Müll. Hal., Syn. Musc. Frond. 2: 103. 1850. Protologue. In regni Mexicani montosis apricis, juxta Toluccam, ad radices montis perpetua nive obtecti, regione frigida, altitudine 1640 hexapodarum. *Humboldt et Bonpland.*

Braunia secunda (Hook.) Bruch & Schimp. var. *crassiretis* Thér., Smithsonian Misc. Collect. 78(2): 24. 1926. Protologue. [Mexico] Morelia, Campanario [State of Michoacán, 2200–2300 meters] [Arsène] 7448. Type. Plants of Mexico, vicinity of Morelia, State of Michoacán, Campanario, 2200 m, 11.1911, *Bro. G. Arsène* 7448 (US, holotype).

Plants medium-sized, in yellow green mats. Primary stems creeping, irregularly branched; leaves reduced, well spaced, ovate, abruptly long-acuminate, erect below, squarrose-recurved above, 0.6–0.8 mm long; cells pluripapillose; rhizoids red brown, in sparse clusters at abaxial side of leaf insertions, not or rarely branched. Secondary stems horizontal and often with lateral stolons, or erect and loosely spreading, 3–5 cm long, irregularly branched; cross section with sclerodermis of 2–5 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, firm- or thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent. Secondary stem and branch leaves erect-imbricate when dry, wide-spreading when wet, oblong-ovate, plicate, 2 mm long, shortly acuminate, shortly decurrent; margins narrowly recurved, often to near the apex, apices sparsely serrulate to erose; costa absent; upper cells subquadrate, short-rectangular to rectangular, 8–17 µm long, thick-walled, strongly sinuose, pluripapillose; basal median cells long-rectangular, 100 × 4 µm, thick-walled, porose, pluripapillose; alar cells short-rectangular, quadrate, or oblate, 6–12 µm long, thick-walled, smooth. Paroicous. Perichaetial leaves erect, elongate. Setae elongate, yellow, becoming red to orange with age, 7–20 mm long. Capsules erect, cylindrical to elliptic, 2 mm long, wrinkled to irregularly furrowed when dry, light brown, narrowed at the mouth, at times strongly constricted at neck; exothecial cells small, red, thick-walled in 10–15 rows below the mouth, becoming lax, irregularly quadrate to short-rectangular below, neck cells small, irregularly subquadrate to short-rectangular; stomata in neck; opercula obliquely conic-rostrate, to 1 mm long; annuli rudimentary, cells often clinging to capsule mouth or operculum; peristome absent. Spores irregularly subspherical to oblong, papillose, 18–26 µm. Calyptrae cucullate, smooth or sparsely hairy, 3.5–4.5 mm long.

Illustrations. Hooker (1818, Tab. 46); Churchill and Linares (1995, Fig. 100 h–k). Figure 7.

Habitat. On shaded rock; 2700 m.

Distribution in Central America. GUATEMALA. Quetzaltenango: *Standley 85253* (F, FH, NY).

World range: Southwestern and South-Central U.S.A.; Mexico; Central America; Caribbean; Western and Northern South America.

Braunia secunda is often considered a widespread species present in Africa (Magill & Rooy 1998), India (Brotherus 1925), and the Neotropics. De Luna (1992) narrowed the circumscription of the species to include only paroicous Neotropical collections that have lanceolate, acuminate leaves with margins recurved to a scabrous dentate apex, and ellipsoid, wrinkled to slightly furrowed capsules. The capsules of *B. andrieuxii* and *B. secunda* are similar in shape, but *B. andrieuxii* is autoicous rather than paroicous. In addition, the leaves of *B. andrieuxii* are broader than those of *B. secunda*, have margins recurved only in the lower half, a shorter, broader leaf apex, and weakly sinuose upper leaf cells. Furthermore, in *B. andrieuxii* the secondary stem and branch tips are often transformed into stolons, while in *B. secunda* stolons generally arise laterally from the secondary stems and branches. *Braunia squarrulosa* is similar to *B. secunda* in leaf shape and in having strongly sinuose upper leaf cells. It differs in having hair-pointed leaves with margins recurved only in the lower half or less.

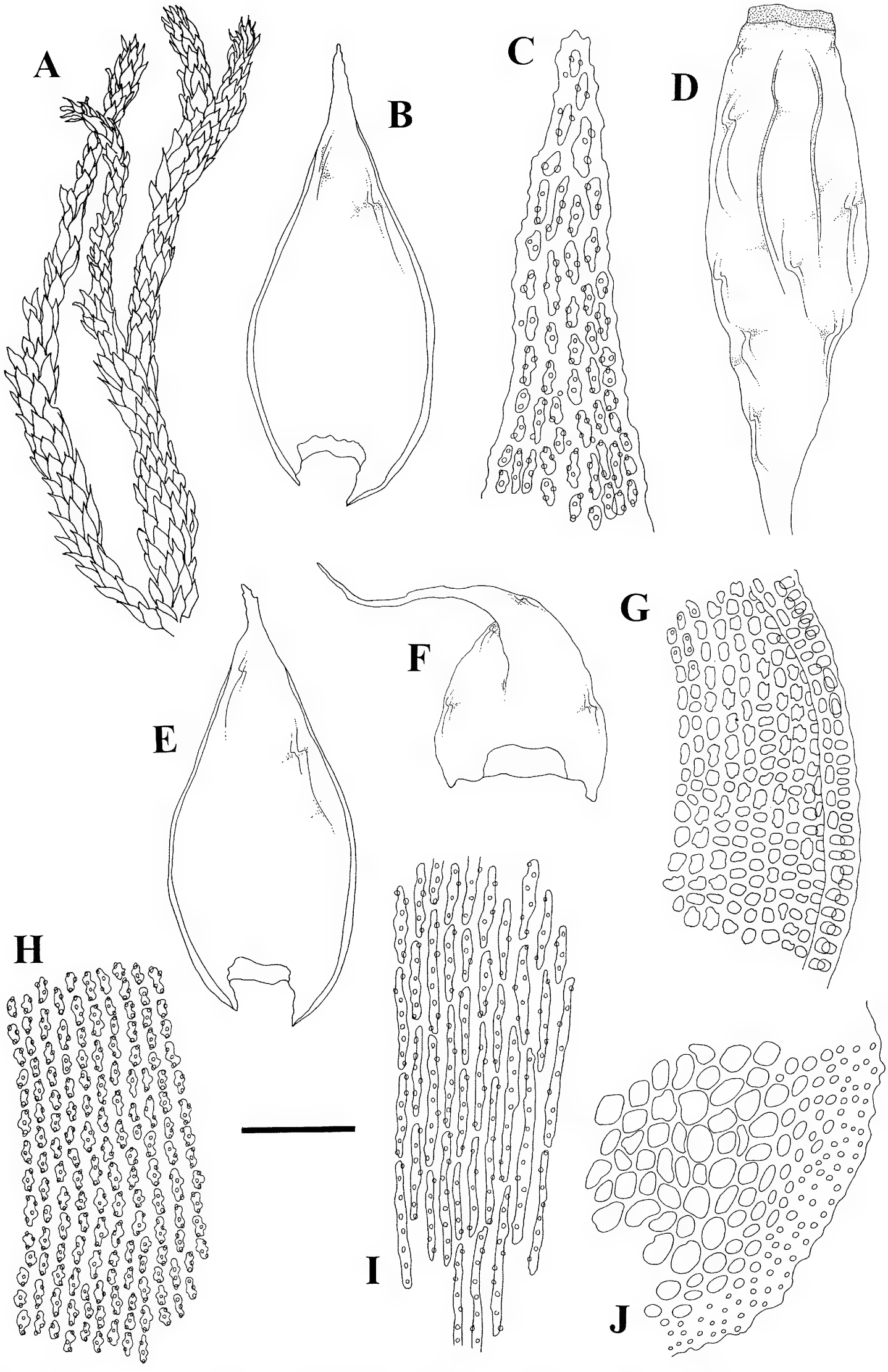


Figure 7. *Braunia secunda*. A. Habit. B & E. Leaves. C. Leaf apex. D. Seta and capsule. F. Stipe leaf. G. Margin at midleaf. H. Upper leaf cells. I. Basal leaf cells. J. Stem in cross section. Scale in mm: bar = 0.06 (C, G, H, I); bar = 0.08 (J); bar = 0.26 (F); bar = 0.5 (B, E); bar = 0.6 (D); bar = 2.2 (A). All figure parts from *Standley 85253*.

3. *Braunia squarrulosa* (Hampe) Müll. Hal., Linnaea 42: 380. 1879. *Harrisonia squarrulosa* Hampe, Linnaea 12: 349. 1838. *Hedwigidium squarrulosum* (Hampe) Bruch & Schimp. *in* B.S.G., Bryol. Eur. 3: 161. 1846 (fasc. 29–30). *Hedwigia squarrulosa* (Hampe) Mitt., J. Linn. Soc., Bot. 12: 407. 1869. Protologue. Inter muscos Mexicanos, terrestris?

Neckera sphaerocarpa Müll. Hal., Syn. Musc. Frond. 2: 105. 1850, illegitimate homonym not *Neckera sphaerocarpa* Hook., 1808. *Braunia sphaerocarpa* Müll. Hal., Bull. Herb. Boissier 5: 201. 1897, new name for *Neckera sphaerocarpa* Müll. Hal. Protologue. Mexico: *C. Ehrenberg*. E Guatemala copiose communicavit *Kegel*.

Neckera liebmanniana Müll. Hal., Syn. Musc. Frond. 2: 668. 1851. *Hedwigia liebmanniana* (Müll. Hal.) Mitt., J. Linn. Soc., Bot. 12: 407. 1869. *Braunia liebmanniana* (Müll. Hal.) Schimp., Mém. Soc. Sci. Nat. Cherbourg 16: 185. 1872. Protologue. Mexico, Pico de Orizaba: *Liebmann*.

Plants medium-sized, in yellow green mats. Primary stems creeping, irregularly branched; leaves well spaced, reduced, ovate, abruptly long-acuminate, erect below, squarrose-recurved above, 0.6–0.8 mm long; rhizoids red brown, in sparse clusters at abaxial side of leaf insertions, not or rarely branched. Secondary stems horizontal and often with lateral stolons, or erect and loosely spreading, 3–10 cm long, irregularly branched; cross section with sclerodermis of 2–5 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, firm- or thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent. Secondary stem and branch leaves erect at base, spreading to squarrose above when dry, spreading to wide-spreading when wet, oblong-ovate, strongly plicate, 2–3 mm long, ending in a slender, hyaline hair-point, shortly decurrent; margins narrowly recurved in the lower 1/2 or less, plane above; apices erose; costa absent; upper cells short-rectangular to rectangular, 8–20 µm long, thick-walled, strongly sinuose, pluripapillose; basal median cells long-rectangular, 98 × 4 µm, thick-walled, porose, pluripapillose; alar cells short-rectangular, quadrate, or oblate, 6–12 µm long, thick-walled, smooth. Autoicous. Perichaetial leaves erect, elongate. Setae elongate, yellow, 3–5 mm long. Capsules erect, globose to subglobose, 1.3–1.7 mm long, somewhat wrinkled when dry, yellowish brown when young, becoming red brown with age, narrowed at the mouth, variously constricted at neck; exothecial cells small, reddish brown, in 5–15 rows below the mouth, becoming larger, oblate, irregularly quadrate to short-rectangular below; neck cells small, irregularly subquadrate to short-rectangular; stomata in neck; opercula obliquely conic-rostrate, to 1 mm long; annuli rudimentary, cells often clinging to capsule mouth or operculum; peristome absent, mouth closed by a membrane; anisosporous. Spores massive, thin-walled, vermicular-papillose, more or less spherical, 60–90 µm, and small, smooth, spherical, 8–10 µm. Massive spores undergoing endosporic germination and becoming multicelluar before dispersal. Calyptrae mitrate-cucullate, sparsely hairy, 3.5–4.5 mm long.

Illustrations. Bartram (1949, Pl. 106 A–C); Sharp *et al.* (1994, Fig. 497 g–i). Figure 8.

Habitat. On bark of trees (*Alnus*, *Juniperus*, *Quercus*, *Cupressus*), rocks (limestone), and soil of trail banks; 1600–3800 m.

Distribution in Central America. GUATEMALA. Huehuetenango: *Standley 82548* (F, FH, NY); Quetzaltenango: *Sharp 2034* (FH, US); Totonicapán: *Standley 62674* (F, FH, NY); San Marcos: *Steyermark 35481* (F, FH, NY). HONDURAS. Lempira: *Allen 12102* (MO, TEFH). COSTA RICA. San José: *Bryotheca Gottingensis 42* (MO). PANAMA. Chiriquí: *Davidse & D'Arcy 10183B* (H, MO, NY, PMA, US).

World range: Mexico; Central America.

Braunia squarrulosa is the most common species of *Braunia* in Central America and unlike the other species is more often found on the bark of trees than on rocks. The species has hair-pointed leaves that are spreading to reflexed above when dry. Its leaves are somewhat pinched below, with margins more broadly recurved than in *B. secunda*, and fairly long, strongly sinuose upper leaf cells. It is the only Central American species with subglobose to globose capsules. Other distinctive features of *B. squarrulosa* include its sparsely hairy calyptrae, short setae, and massive spores.

The spores of *B. squarrulosa* are dimorphic: small, apparently unviable ones, and massive, viable ones that reach 90 µm in diameter. The massive spores are retained in the capsules and undergo precocious, endosporic germination. The diaspores in this species are multicellular, endosporic protone-

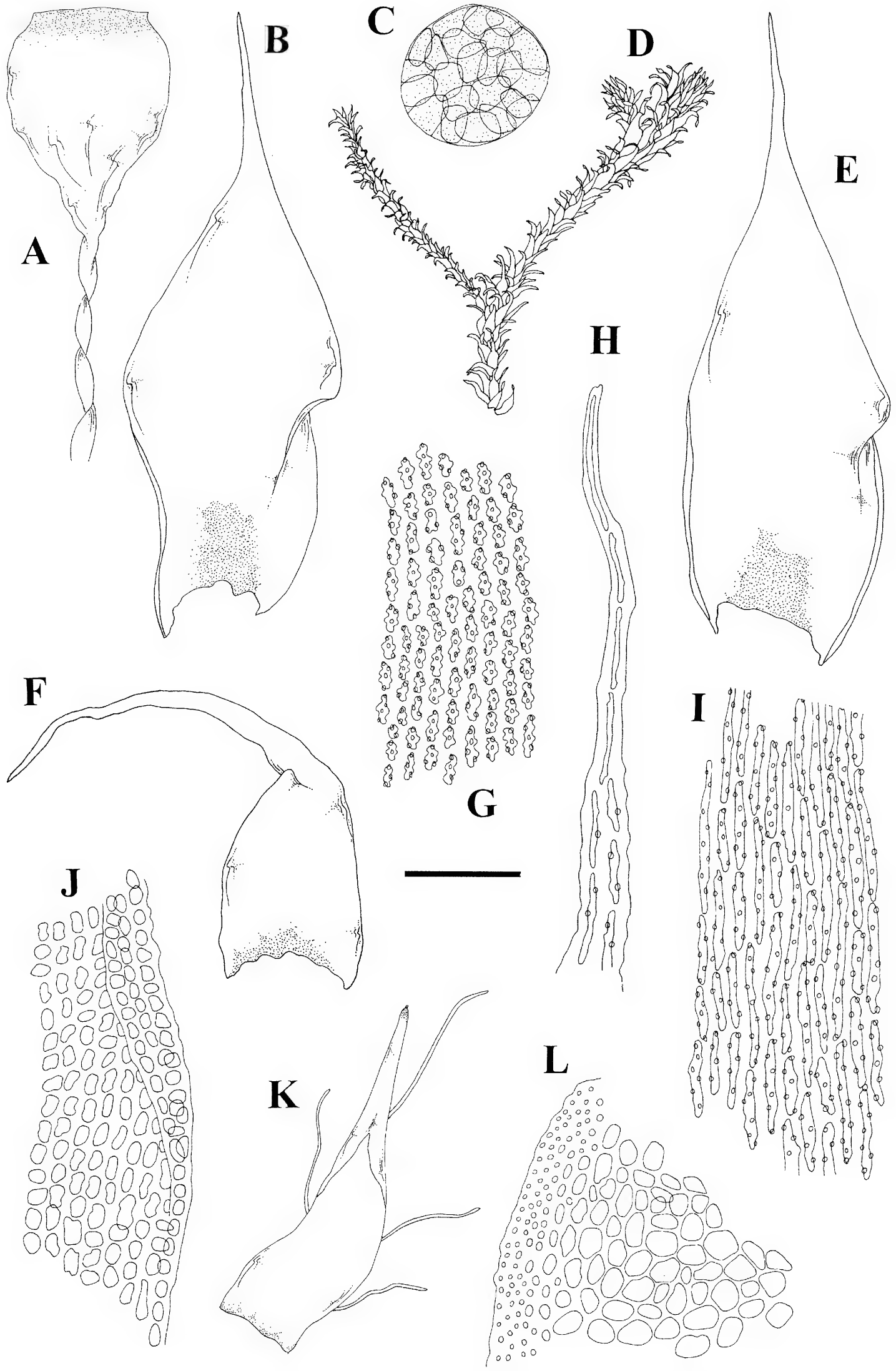


Figure 8. *Braunia squarrulosa*. A. Seta and capsule. B & E. Leaves. C. Endosporic protonemata. D. Habit. F. Stipe leaf. G. Upper leaf cells. H. Leaf apex. I. Basal cells. J. Margin near leaf base. K. Calyptra. L. Stem in cross section. Scale in mm: bar = 0.06 (C, G, I, J); bar = 0.08 (L); bar = 0.26 (F); bar = 0.5 (B, E); bar = 0.9 (A, K); bar = 4.0 (D). A, C from *Hermann 26429*; B, E, H from *Holz CR99-905*; F, L from *Standley 82593*; K from *Steyermark 50604*; all other figure parts from *Holz 42*.

mata. This type of diaspore is found sporadically throughout the mosses (see Allen 1987a, c). Allen (1987e) demonstrated that in *Drummondia* the condition shortened the time between dispersal and the formation of leafy gametophytes. The presence in *B. squarrulosa* of a membranous structure that keeps the capsule mouth closed after operculum dehiscence may also be correlated with this type of spore germination.

All other Central American species of *Braunia* differ from *B. squarrulosa* in having erect, imbricate leaves, cylindrical to elliptic capsules, and smaller spores. In some collections of *B. squarrulosa* the leaves are weakly spreading at the tips, and have poorly developed hair-points. These collections can be distinguished from *B. andrieuxii* and *B. secunda* by the combination of strongly sinuose upper leaf cells and weakly recurved leaf margins. In *B. andrieuxii* the leaf margins are weakly recurved, but the upper leaf cells are more or less straight-walled, while *B. secunda* has strongly sinuose upper leaf cells, but leaf margins recurved to near the apex.

Braunia plicata (Mitt.) A. Jaeger is a Mexican species that approaches an expression of *B. squarrulosa* that is nomenclaturally centered on *B. liebmanniana* and has fairly broad, imbricate leaves. *Braunia plicata* differs from *B. squarrulosa* in having cylindrical to ellipsoid capsules, and broader, more strongly plicate leaves with margins recurved to near the apex. *Hedwigidium imberbe* differs from *B. squarrulosa* in having immersed capsules. The leaves in both species, however, are similar in shape, and *H. imberbe* can have hyaline-tipped or hair-pointed leaves. Collections that lack sporophytes can be difficult to place to species, but in *H. imberbe* the leaves are erect-imbricate when dry, have strongly recurved leaf margins, and often sparsely serrate hair-points.

2. *Hedwigia* P. Beauv., Mag. Encycl. 5: 304. 1804, conserved name.

Plants medium-sized to robust, in green to yellow green, dense, often hoary, rigid tufts or mats. Primary stems short, creeping, irregularly branched; leaves reduced; rhizoids red brown, in sparse clusters at abaxial side of leaf insertions, not or rarely branched. Secondary stems erect and loosely spreading, irregularly branched, rarely with lateral stolons; cross section with sclerodermis and enlarged, thick-walled cortical cells, central strand absent; paraphyllia absent; pseudoparaphyllia foliose. Secondary stem and branch leaves erect-appressed or erect at base and wide-spreading above to secund when dry, erect-spreading to spreading when wet, not plicate, oblong-ovate, acute to acuminate, apices ending in long or short, broad or narrow, hyaline, variously papillose acumina, shortly decurrent; margins plane or narrowly recurved to midleaf, plane, erect, or narrowly incurved below apices, often sparsely spinose-serrate at the apex; costa absent; upper cells short-rectangular to subquadrate, thick-walled, variously pluripapillose; basal median cells long-rectangular, very thick-walled, porose, pluripapillose, hyaline to yellow orange at base; alar cells in numerous rows at basal angles, short-rectangular, quadrate, or oblate, very thick-walled, smooth, reddish brown, at times yellow orange. Autoicous. Perigonia gemmate, sessile on secondary stems and branches. Perichaetia terminal, perichaetial leaves erect, elongate, overtopping the capsules, margins entire or with long, hyaline, pluripapillose cilia. Setae short. Capsules immersed, erect, cupulate, wide-mouthed, tapering to short wrinkled necks; exothecial cells small, reddish brown below the mouth, becoming larger, oblate, irregularly subquadrate below, neck cells small; cryptoporic stomata in neck; opercula plano-convex or umbonate; annuli rudimentary; peristome absent. Spores vermiculate-papillose, irregularly shaped, with tri-radiate mark on one side. Calyptrae conic-cucullate or conic-mitrate, smooth, not or at times sparsely hairy.

Hedwigia has often been considered a monospecific genus (see Hedenäs 1994 and Buck & Norris 1996), but presently it contains at least five taxa (*H. ciliata* (Hedw.) P. Beauv., *H. ciliata* var. *leucophaea* Bruch & Schimp. *in* B.S.G., *H. detonsa* (M. Howe) W. R. Buck & D. H. Norris, *H. nivalis* (Müll. Hal.) Mitt., and *H. stellata* Hedenäs). The genus lacks a stem central strand, paraphyllia, leaf costa, and peristome. Its primary, creeping stems are so poorly developed they are often difficult to demonstrate, and its secondary stems and branches rarely produce stolons. *Hedwigia* characteristically has broadly ovate, acuminate leaves that end in broad, hyaline acumina, densely papillose leaf cells, immersed, cupulate capsules, and cryptoporic stomata. Although *H. detonsa* has entire perichaetial leaves, all other species of *Hedwigia* have long-ciliate perichaetial leaves.

Hedwigidium and *Hedwigia* have immersed capsules, and their gametophytes are very similar. *Hedwigidium* differs from *Hedwigia* in often having stoloniferous gametophytes, concolorous or narrowly hair-pointed leaf apices, longer, broadly oblong to subglobose, furrowed capsules, and phaneroporic stomata.

Braunia is immediately separated from *Hedwigia* by its long-exserted capsules. In Central America, the gametophytes of *Braunia* can also be distinguished from *Hedwigia* by their concolorous or narrowly hair-pointed leaf apices. There are, however, some *Braunia* species outside the region (*i.e.*, *B. diaphana* (Müll. Hal.) A. Jaeger) that have long, broad, hyaline leaf acumina identical to those of *Hedwigia*. The gametophytes of *Braunia*, like those of *Hedwigidium*, often have stoloniferous shoots from its secondary stems and branches, and this feature can be used to separate *Braunia* from *Hedwigia*. In addition, the leaves of *Braunia* are often plicate, while those of *Hedwigia* are smooth.

The name *Hedwigia* commemorates Johannes Hedwig (10 December 1730–18 February 1799; but see Margadant 1968), a German bryologist whose posthumous book *Species Muscorum Frondosorum* serves as the nomenclatural starting point for all moss names except Sphagnaceae.

Hedwigia nivalis (Müll. Hal.) Mitt., J. Linn. Soc., Bot. 12: 405. 1869. *Pilotrichum nivale* Müll. Hal., Syn. Musc. Frond. 2: 165. 1851. Protologue. Venezuela, prov. Merida, in montibus nivosis: *Mortiz No. 174*. Type. Venezuela, Merida, *Mortiz 174* (NY, isotype).

Pilotrichum subrevolutum Müll. Hal., Syn. Musc. Frond. 2: 165. 1851. *Hedwigia subrevoluta* (Müll. Hal.) Mitt., J. Linn. Soc., Bot. 12: 405. 1869. *Hedwigia albicans* Lindb. fo. *subrevoluta* (Müll. Hal.) M. Fleisch., Hedwigia 61: 403. 1920. Protologue. Mexico, *Harrisoniae secundae* associatum ad saxa pr. Malpays de la Joya: *Schiede*. In locis non indicatis ibidem legit *C. Ehrenberg*.

Plants medium-sized to robust, in green to yellow green, dense, hoary, rigid tufts or mats. Primary stems short, creeping, irregularly branched; leaves well spaced, ovate, abruptly acuminate, erect below, recurved above, apex not hyaline, 0.7–1.0 mm long; rhizoids red brown, in sparse clusters at abaxial side of leaf insertions, not or rarely branched. Secondary stems erect and loosely spreading, 2–6 cm long, irregularly branched, rarely with lateral stolons; cross section with sclerodermis of 2–4 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow, thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia foliose. Secondary stem and branch leaves erect-appressed, apices at times wide-spreading or secund when dry, erect-spreading to spreading when wet, not plicate, oblong-ovate, 2.0–2.5 mm long, acute to acuminate, apices ending in long, broad, hyaline, pluripapillose acumina, sparsely spinose-serrate at the apices, shortly decurrent; margins plane or narrowly recurved at base, plane at midleaf, narrowly incurved below apex; costa absent; upper cells short-rectangular to subquadrate, 8–16 × 5–7 µm, thick-walled, papillae 1–2(–3) on the abaxial surface, stout, at times branched; basal median cells long-rectangular, 40–70 × 2.5–7 µm, very thick-walled, porose, pluripapillose, hyaline to yellow orange at base; alar cells in numerous rows at basal angles short-rectangular, quadrate, or oblate, very thick-walled, papillose, reddish brown, at times yellow orange, 8–18 × 7–10 µm. Autoicous. Perigonia gemmate, sessile on secondary stems and branches. Perichaetia terminal, perichaetial leaves erect, elongate, overtopping the capsules, upper margins with long, hyaline, pluripapillose cilia. Setae short, to 1.0 mm long. Capsules immersed, erect, cupulate, 1 mm long, smooth, red brown, wide-mouthed, tapering to a short wrinkled neck; exothecial cells small, reddish brown, in 5–10 rows below the mouth, larger, oblate, irregularly subquadrate below, neck cells small; cryptoporic stomata in neck; opercula plano-convex, at times umbonate, 0.5 mm high; annuli rudimentary; peristome absent. Spores vermiculate-papillose, irregularly shaped, 22–26 µm, brown. Calyptrae conic-cucullate, smooth, naked, 1 mm long.

Illustrations. Churchill and Linares (1995, Fig. 100 a–g, as *H. ciliata*); Magill and Rooy (1998, Fig. 151 12–21, as *H. ciliata*). Figure 9.

Habitat. On exposed or shaded rocks and shaded banks; 2280–3500 m.

Distribution in Central America. GUATEMALA. Huehuetenango: *Vogel B-9008* (NY, US); Quetzaltenango: *Standley 85256* (F, FH, NY). COSTA RICA. San José: *Holz CR 03-378A* (MO).

World range: Southwestern, and South-Central U.S.A.; Mexico; Caribbean; Western, Northern, and Southern South America, Brazil; Middle Asia, Southern Africa, Western Indian Ocean; Australia, New Zealand.

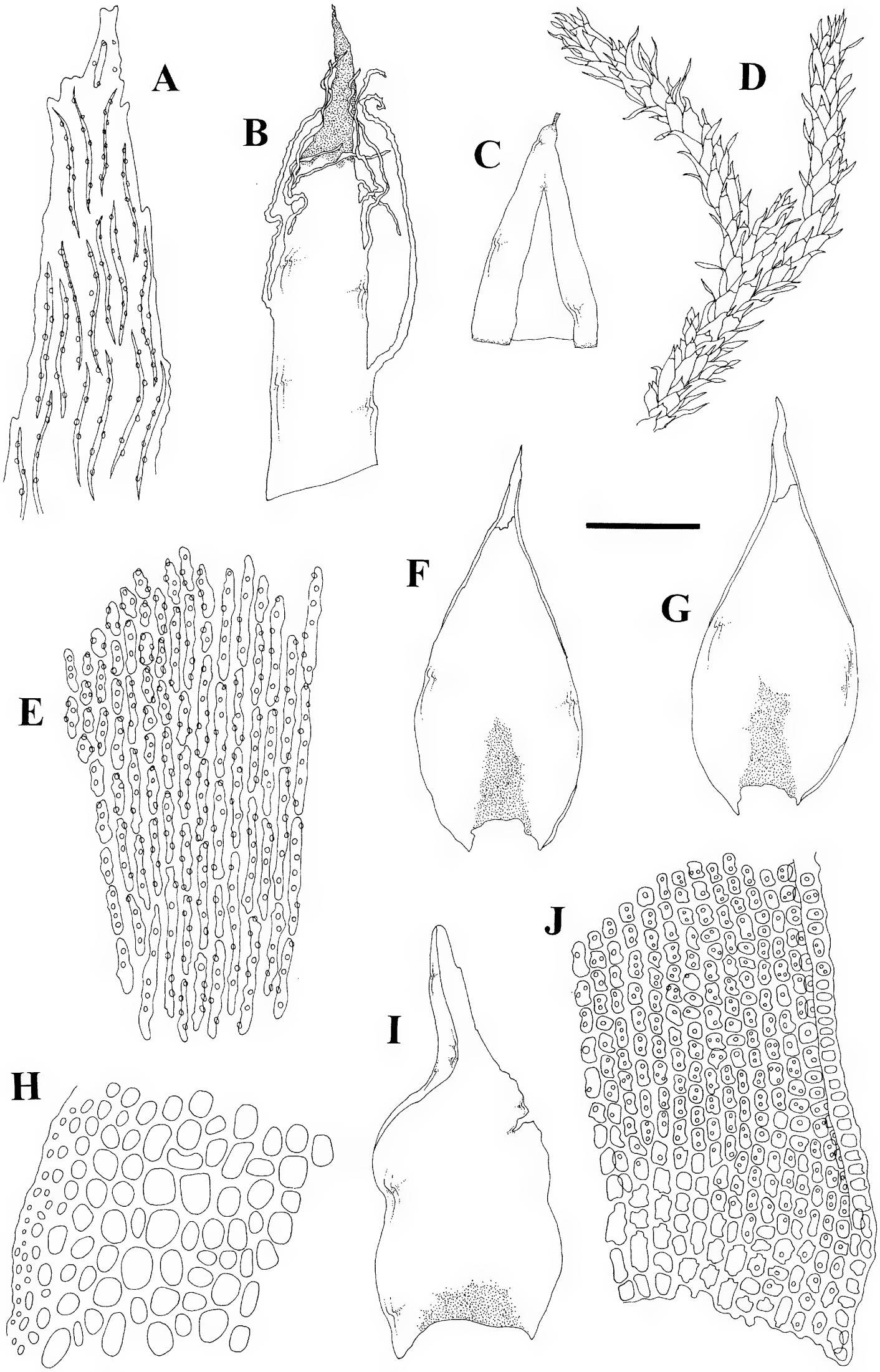
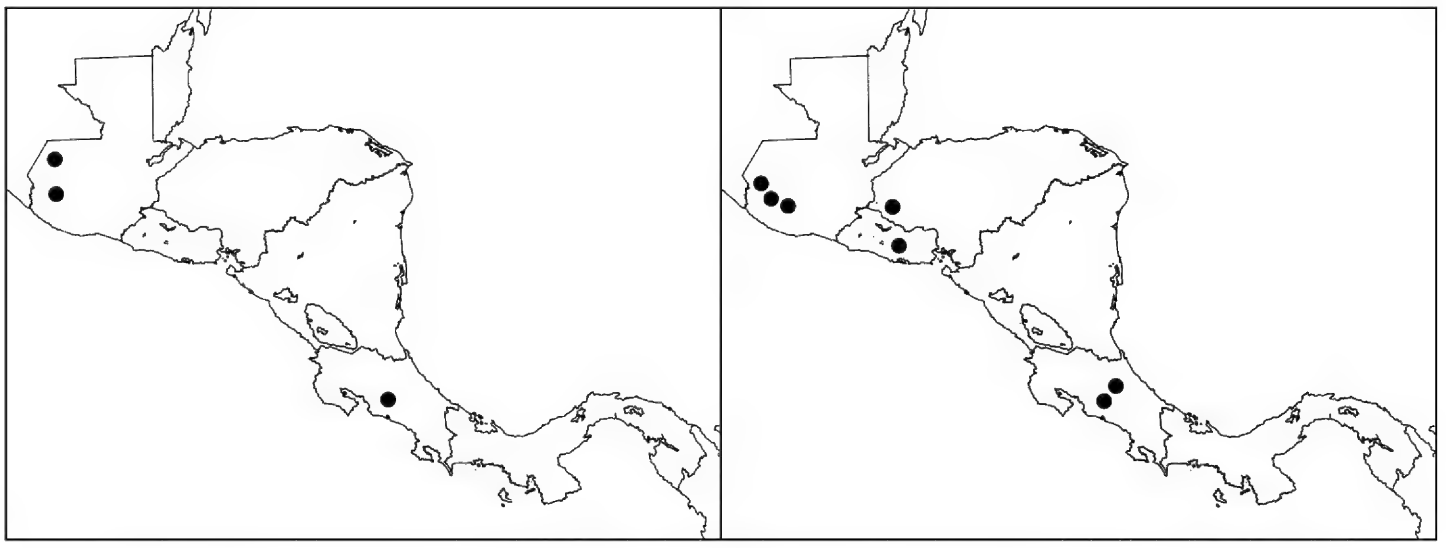


Figure 9. *Hedwigia nivalis*. A. Leaf apex. B. Perichaetial leaf. C. Calyptra. D. Habit. E. Median leaf cells. F & G. Leaves. H. Stem in cross section. I. Primary stem leaf. J. Basal leaf cells. Scale in mm: bar = 0.06 (A, E, J); bar = 0.08 (H); bar = 0.34 (C); bar = 0.26 (I); bar = 0.6 (B, F, G); bar = 2.5 (D). A from *Davidse 34179*; B from *Pursell 5003*; C from *Whittemore 3959*; I from *Knobloch*; all other figure parts from *Vogel B-9008*.



Hedwigia nivalis *Hedwigidium imberbe*

Hedwigia nivalis is distinguished from all other members of the Hedwigiaceae in Central America by its broad, long, hyaline leaf apices. There are Central American members of *Braunia* with consistently hyaline hair-pointed leaves and *Hedwigidium* at times can have such leaves, but in these species the hyaline portion of the leaf is always restricted to the hair-points. *Racomitrium lanuginosum* (Hedw.) Brid. (recently found in Costa Rica) has leaf apices similar to *H. nivalis*, and both species often have a hoary appearance when dry. The presence of a long single costa in the leaves of *R. lanuginosum* distinguishes it from *H. nivalis*. Other distinctive features of *H. nivalis* include its long-ciliate perichaetial leaves, immersed, cupulate capsules, and immersed stomata.

In Central America this species has been called *Hedwigia ciliata* (Hedw.) P. Beauv. var. *leucophaea* Bruch & Schimp. *in* B.S.G. However, Buck and Norris (1996) found that typical *H. ciliata* differed from Latin American material of *Hedwigia* in having leaves with margins recurved below but plane above, 2–4 papillae on the abaxial side of the leaf cells, and narrower, less papillose, hyaline leaf apices. *Hedwigia nivalis* is the oldest name for the Latin American taxon. *Hedwigia ciliata* var. *leucophaea*, as noted by Buck and Norris (1996), can be difficult to distinguish from *H. nivalis*. In *Hedwigia ciliata* var. *leucophaea* the leaves are more oblong than those of *H. nivalis*, they have exceptionally long, hyaline leaf acumina (22%–55% of the leaf length, Hedenäs 1994), and often the leaf apex is channeled, *i.e.*, has erect margins. *Hedwigia nivalis* can also have long hyaline leaf acumina, but this is not an essential feature of the species, and at times the hyaline acumina are as short as those of *H. ciliata*. *Hedwigia nivalis* is best distinguished from *H. ciliata* var. *leucophaea* by the presence of incurved upper leaf margins and non-hairy calyptrae. As noted above, the leaf apex of *H. ciliata* var. *leucophaea* can be channeled, but the upper leaf margins are plane or erect rather than incurved, and its calyptrae are hairy.

Hedwigia stellata occurs in southern California and may be found in Central America. It is similar to *H. nivalis* in having erect to incurved upper leaf margins, but differs in its longer, narrower, hyaline leaf apices that are smooth above and wide-spreading to squarrose when dry, and upper abaxial leaf cells with one to two long, stout, branched papillae.

The above world distribution of *H. nivalis* may be incomplete and/or inaccurate due to taxonomic confusion between *H. nivalis* and *H. ciliata* var. *leucophaea*.

3. *Hedwigidium* Bruch & Schimp. *in* B.S.G., Bryol. Eur. 3: 155 (fasc. 29–30).

Plants medium-sized to somewhat robust, in green, yellow green, or reddish yellow, loose or dense, tufts or mats. Primary stems short, creeping, irregularly branched; leaves well spaced, scale-like, ovate, abruptly long-acuminate, erect below, squarrose-recurved above; rhizoids red brown, in sparse clusters at abaxial side of leaf insertions, not or rarely branched. Secondary stems erect and loosely spreading, irregularly branched, often with lateral stolons; cross section with sclerodermis and enlarged cortical cells, central strand absent; paraphyllia absent; pseudoparaphyllia foliose. Secondary stem and branch leaves erect-imbricate when dry, erect-spreading when wet, oblong-ovate,

slenderly acuminate, apices concolorous or hyaline-tipped, shortly decurrent, not or weakly plicate, lateral stolon leaves often long hair-pointed; apices sparsely serrate; margins narrowly recurved to near the apices; costa absent; cells thick-walled, sinuose, pluripapillose, upper cells short-rectangular to subquadrate or oblate; basal median cells long-rectangular, yellow; basal marginal cells short-rectangular, quadrate, or oblate, smooth, dark reddish brown. Autoicous. Perigonia lateral. Perichaetia terminal, perichaetial leaves erect, elongate, overtopping the capsules. Setae short. Capsules immersed, erect, broadly oblong to subglobose, furrowed when wet or dry, red brown; phaneroporic stomata in neck; opercula obliquely conic-rostrate; annuli rudimentary; peristome absent. Spores vermiculate-papillose, irregularly shaped, 20–24 μm, brown. Calyptrae conic-mitrate, 2–3-lobed, smooth.

Hedwigidium is a monospecific genus found throughout the Southern Hemisphere as well as Europe and Mexico. The sporophytes of *Hedwigidium* and *Hedwigia* are immersed, and the genera are sometimes (Nyholm 1960; Scott & Stone 1976; Smith 1978; Casas 1991; Hedenäs 1998; Cortini Pedrotii 2001) considered synonymous. The gametophytes of *Hedwigidium* differ from those of *Hedwigia* in having stoloniferous stems and branches and leaves with concolorous or narrowly hair-pointed apices. In contrast the stems and branches of *Hedwigia* rarely produce stolons, and its leaves have very broad, hair-pointed apices. *Braunia* differs from *Hedwigidium* in having long-exserted capsules, but their gametophytic characters matched so closely that the two genera are sometimes difficult to distinguish from one another. *Pseudobraunia* is found nearby in California and, like *Braunia*, it too has long-exserted capsules. *Pseudobraunia* further differs from *Hedwigidium* in having leaves with consistently long, hyaline hair-points and single, long, stout leaf cell papillae.

The name *Hedwigidium* combines the generic name *Hedwigia* with the diminutive Greek suffix *-idium*.

Hedwigidium imberbe (Sm.) Bruch & Schimp. *in* B.S.G., Bryol. Eur. 1: 157 (fasc. 29–30). 1846. *Gymnostomum imberbe* Sm., Engl. Bot. 2237. 1810. *Anictangium imberbe* (Sm.) Hook. & Taylor, Muscol. Brit. 14. 1818. *Hedwigia imberbis* (Sm.) Spruce, Musci Pyren. 263. 1847. Protologue. Discovered on dry rocks upon mountains in the west of Ireland by Miss Hutchins, who in 1809 sent specimens to Mr. Turner, which he has kindly communicated to us.

Plants medium-sized to somewhat robust, in green, yellow green, or reddish yellow, loose or dense tufts or mats. Primary stems short, creeping, irregularly branched; leaves well spaced, ovate, abruptly long-acuminate, erect below, squarrose-recurved above, 0.6–0.8 mm long; rhizoids red brown, in sparse clusters at abaxial side of leaf insertions, not or rarely branched. Secondary stems erect and loosely spreading, 2–10 cm long, irregularly branched, often with lateral stolons; cross section with sclerodermis of 2–5 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow, thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia foliose. Secondary stem and branch leaves erect-imbricate when dry, erect-spreading when wet, oblong-ovate, 1.5–2 mm long, slenderly acuminate, apices concolorous or hyaline-tipped, shortly decurrent, not or weakly plicate, lateral stolon leaves often long hair-pointed; apices sparsely serrate; margins narrowly recurved to near the apex; costa absent; upper cells short-rectangular to subquadrate or oblate, 6–14 × 4–6 μm, very thick-walled, sinuose, pluripapillose; basal median cells long-rectangular, 40–64 × 4 μm, very thick-walled, porose, pluripapillose, yellow; alar cells in numerous rows at basal angles short-rectangular, quadrate, or oblate, very thick-walled, smooth, dark reddish brown. Autoicous. Perigonia lateral. Perichaetia terminal, perichaetial leaves erect, elongate, overtopping the capsules. Setae short, yellow becoming red with age, 1 mm long. Capsules immersed, erect, broadly oblong to subglobose, 1.5–2.0 mm long, strongly furrowed when wet or dry, red brown, slightly narrowed at the mouth, tapering to the seta; exothecial cells small, reddish brown, in 5–10 rows below the mouth, larger, oblate, irregularly subquadrate below, neck cells small; stomata in neck; opercula obliquely conic-rostrate, 0.5 mm long; annuli rudimentary; peristome absent. Spores vermiculate-papillose, irregularly shaped, 20–24 μm, brown. Calyptrae conic-mitrate, 2–3-lobed, reddish yellow, smooth, 1.5 mm long.

Illustrations. Bartram (1949, Fig. 105 H–J); Scott and Stone (1976, Pl. 68); Sharp *et al.* (1994, Fig. 496); Churchill and Linares (1995, Fig. 101 a–f). Figure 10.

Habitat. On rocks, non-calcareous boulders, cliffs, and sandy banks; 2700–3768 m.

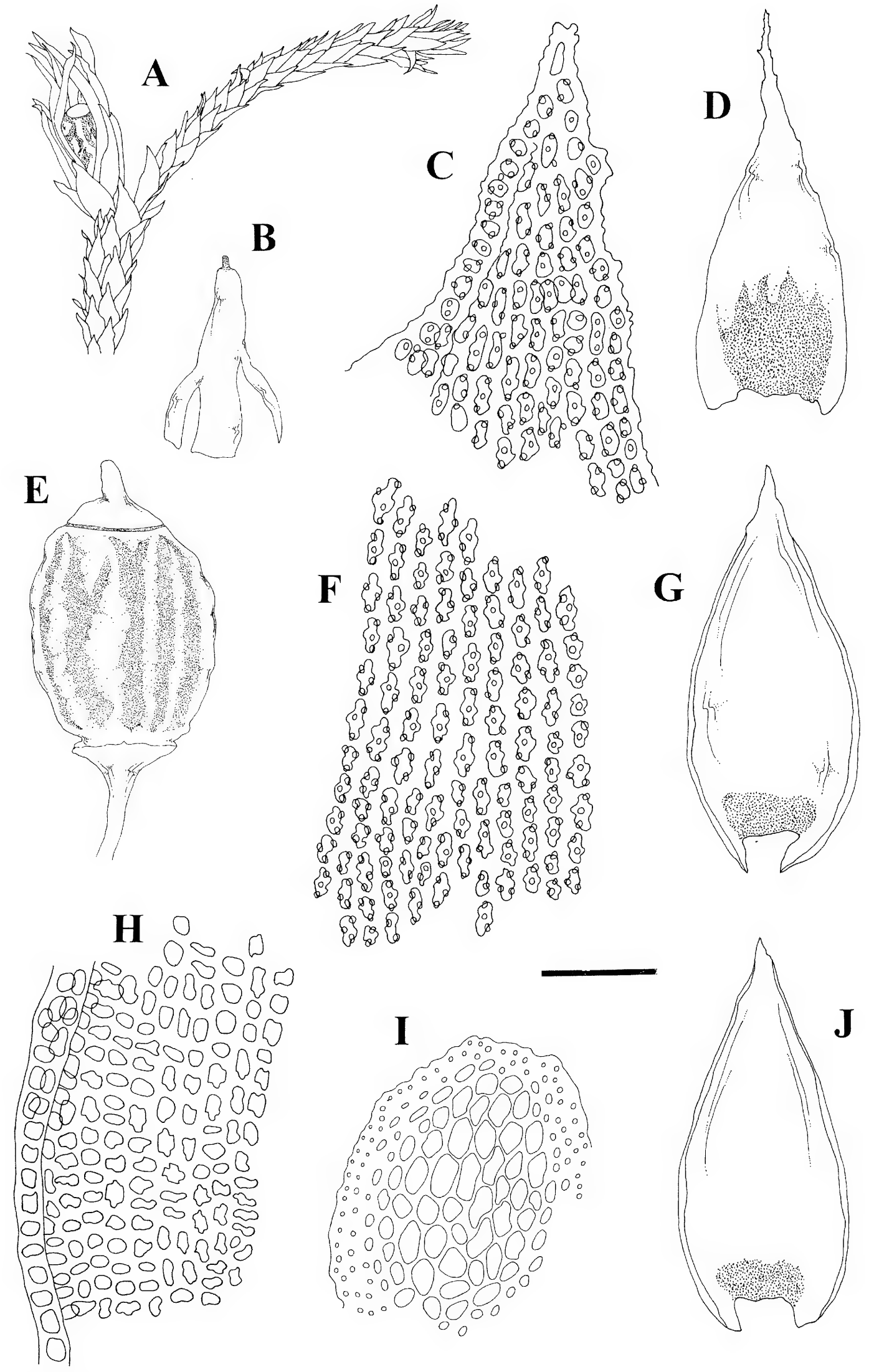


Figure 10. *Hedwigidium imberbe*. A. Habit. B. Calyptra. C. Leaf apex. D. Primary stem leaf. E. Seta and capsule. F. Median leaf cells. G & J. Leaves. H. Basal leaf cells. I. Stem in cross section. Scale in mm: bar = 0.05 (C, F, H); bar = 0.08 (I); bar = 0.2 (D); bar = 0.5 (G, J); bar = 0.8 (B, E); bar = 2.5 (A). B & E from *Holz & Sipman CR99-913*; all other figure parts from *Allen 12119*.

Distribution in Central America. GUATEMALA. Quetzaltenango: *Standley 85751* (F, FH, NY); San Marcos: *Sharp 5449* (F, NY); Sololá: *Steyermark 47467* (F, FH, NY, US). EL SALVADOR. San Vicente: *Winkler 413* (TUB, Winkler 1965). HONDURAS. Lempira: *Allen 12255* (MO, TEFH). COSTA RICA. Cartago: *Bryotheca Gottingensis 41* (MO); San José: *Griffin et al. 019982* (MO, NY, US).

World range: Mexico; Central America; Caribbean; Western, Northern and Southern South America, Brazil; Northern, Southwestern, Middle, and Southeastern Europe; West-Central, East, and South Tropical Africa, Southern Africa, Western Indian Ocean; Indian Subcontinent; Australia, New Zealand.

Hedwigidium imberbe is fairly common in Central America on rocks at high elevations. It has erect-imbricate leaves with usually concolorous apices, but the branch leaves can sometimes be hyaline-tipped and the stolon leaves are often long hair-pointed. Other critical gametophytic features of the species include its strongly recurved leaf margins, long, sinuose upper leaf cells, low leaf cell papillae scattered over the cell lumina, and exceptionally well-differentiated, commonly dark red cells in the alar regions. The species is autoicous, with gemmate perigonia occurring close to the perichaetia, and collections often have sporophytes. The sporophytes are not always evident because they are deeply immersed, but they can be found because the perichaetial leaves are greatly enlarged.

Although *Hedwigidium imberbe* and *Hedwigia nivalis* are similar in having immersed capsules, their gametophytes are distinctly different. The leaves of *Hedwigidium imberbe* have concolorous or narrowly hair-pointed apices with multiple, low papillae scattered over the leaf cells, and its perichaetial leaves are entire. In *Hedwigia nivalis* the leaves have very broad hair-pointed apices, and high, stout leaf cell papillae, and the perichaetial leaves are ciliate.

Braunia differs from *Hedwigidium imberbe* in having long-exserted capsules, but collections that lack sporophytes can be difficult to place to genus. In Central America *B. andrieuxii* differs from *H. imberbe* in having leaf margins recurved only in the lower half or less and shorter, straight-walled upper leaf cells, while *B. squarrulosa* differs in having leaves with long hyaline hair-points that are strongly reflexed when dry. The leaves of *Braunia secunda* are quite similar to those of *H. imberbe* in stance, shape, apex form, and in having strongly recurved leaf margins. The basal leaf cells of *H. imberbe*, however, are strongly red colored in the alar regions and relatively short in the median regions. In contrast, the basal cells of *B. secunda* are yellowish in the alar regions and relatively long in the median regions, but these basal leaf cell distinctions can be difficult to make without previous experience with the species.

Hedwigidium imberbe has generally been associated with the older *Hedwigia integrifolia* P. Beauv. since Hooker and Taylor (1818) first synonymized the two species (as *Anictangium imberbe*). Jones (1933), however, considered *Hedwigia integrifolia* a synonym of *Hedwigia ciliata*. *Hedwigia integrifolia* clearly is not a synonym of *Hedwigidium imberbe* for two reasons: its type came from North America and it is described as having ciliate perichaetial leaves. *Hedwigidium imberbe* does not occur in North America and its perichaetial leaves are entire. It seems likely Jones (1933) was correct in treating *Hedwigia integrifolia* as a synonym of *Hedwigia ciliata*. Not only do both taxa have ciliate perichaetial leaves, but Palisot de Beauvois (1805) considered *H. integrifolia* very close to or a variety of *Hedwigia filiformis* (Mich.) P. Beauv. Michaux (1803) considered *H. filiformis* to differ from *H. ciliata* only in being a smaller, more slender plant with non-scarious leaf apices.

RHACOCARPACEAE

Rhacocarpaceae Kindb., Bot. Centralbl. 77: 55. 1899.

Plants in glaucous green, greenish yellow, or reddish yellow mats. Primary stems inconspicuous, sympodially branched; rhizoids clustered at base of sympodial branches. Secondary stems prominent, prostrate or erect, irregularly branched from all sides of the stems; cross section with sclerodermis, enlarged, thick-walled cortical cells, central strand absent; paraphyllia absent; pseudoparaphyllia absent; rhizoids absent. Secondary stem and branch leaf cells linear-flexuose, or oval, thick-walled, porose, densely covered by a fine, papillose reticulum, marginal cells usually longer, narrower, smooth forming a distinct border, cells at the insertions smooth, linear, strongly porose, yellow to red; alar cells extensively developed, oblong to subquadrate, red, thick-walled and porose or hyaline, thin-walled and not porose; costa absent. Dioicous. Perigonia gemmate, lateral on secondary stems and branches. Perichaetia terminal; leaves erect, elongate, cells elongate-flexuose, strongly porose, smooth, yellow red; alar cells not differentiated. Setae elongate, smooth or papillose below the capsules. Capsules erect, ovoid, irregularly furrowed, wide-mouthed, constricted at neck, cells in neck, isodiametric, very thick-walled, mammillose-bulging; stomata on neck, deeply immersed; opercula obliquely long-rostrate; annuli rudimentary; peristome absent. Spores tetrahedral, trilete scar present. Calyptrae cucullate, smooth.

The Rhacocarpaceae are based upon a unique leaf ornamentation. The leaf cells are inconspicuously prorate and covered by a perforate reticulum described as a ". . . thick cuticle giving a very ceramic appearance" (Robinson 1975). It is unclear how a perforate reticulum could be deposited on the outside leaf surface. Robinson (1971b) suggested the perforations may result from a partial deposition before leaf elongation was complete. There are two genera now placed in the Rhacocarpaceae: *Pararhacocarpus* J.-P. Frahm and *Rhacocarpus* (Goffinet *et al.* 2009). However, the reasons for including *Pararhacocarpus* in the family are unclear since the genus lacks a perforate reticulum on its leaf cells and its sporophytes are unknown. Frahm (1996) in his original treatment of *Pararhacocarpus* considered the genus *incertae sedis*.

Rhacocarpus has been associated with the Leucodontales, and is often placed in the Hedwigiaceae (Walther 1983; Vitt 1984). Buck and Vitt (1986) recognized the Rhacocarpaceae and placed them near the Pterobryaceae on the basis of their well-developed alar cells and furrowed capsules. De Luna (1990) also excluded *Rhacocarpus* from the Hedwigiaceae because it has filamentous rather than globular protonemata. Buck (1995) proposed a very different family relationship for *Rhacocarpus*. He placed it in the Dicranales near the Dicnemonaceae for five reasons: (1) presence of terminal perichaetia; (2) scale leaves covering branch primordia; (3) bordered leaves with well-developed alar cells, and thick-walled, porose laminal cells; (4) ecostate leaves; and (5) absence of primary stems. Although he considered the two groups to have similar axillary hairs, in *Rhacocarpus* the axillary hairs are two cells long while those of the Dicnemonaceae vary from 3–15 cells long. Frahm *et al.* (1997) considered the Rhacocarpaceae closely related to the Hedwigiaceae on the basis of morphological, molecular, and flavonid chemistry evidence.

The Rhacocarpaceae are here retained in the Leucodontaceae near the Hedwigiaceae or Cryphaeaceae. There are nine characteristics that support this placement: (1) terminal perichaetia; (2) a primary/secondary stem system (see discussion below); (3) unbranched rhizoids present only in clusters at the base of secondary stems; (4) absence of stem central strand; (5) leaves with well-developed alar cells; (6) ecostate leaves; (7) capsule shape; (8) eperistomate capsules; and (9) deeply immersed stomata.

1. *Rhacocarpus* Lindb., Oefvers. Förh. Kongl. Svenska Vetensk.-Akad. 19(10): 607. 1862 [1863].

Harrisonia Spreng., Syst. Veg. 4(1): 145. 1827, illegitimate homonym. Not *Harrisonia* R. Br. *ex* A. Jussieu, Mém. Mus. Hist. Nat. 12: 517. 1825.

Plants medium-sized, in glaucous green, greenish yellow, or reddish yellow mats. Primary stems inconspicuous, sympodially branched, leaves reduced; rhizoids rare, densely clustered at base of sympodial branches, red, smooth, more or less unbranched. Secondary stems prominent, prostrate or

erect, irregularly branched from all sides of the stems; cross section with sclerodermis, enlarged, thick-walled cortical cells, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, apical cell cylindrical-oblong, basal cell subquadrate, red. Secondary stem and branch leaves oblong, broadly elliptic, or lanceolate, at times panduriform, erect to erect-spreading when dry, erect-spreading when wet, hair-pointed, apiculate, or broadly acute, decurrent; margins often narrowly recurved at base and broadly incurved above, serrulate or entire; costa absent; cells linear-flexuose, or oval, thick-walled, porose, densely covered by a finely papillose reticulum; marginal cells usually longer, narrower, smooth, forming a distinct border from 1/2 or the entire leaf length, rarely border absent; cells at the insertions smooth, linear, strongly porose, yellow to red; alar cells extensively developed, oblong to subquadrate, red, thick-walled and porose or hyaline, thin-walled and not porose. Dioicous. Perigonia gemmate, lateral on secondary stems and branches. Perichaetia terminal; leaves erect, elongate, long hair-pointed, cells elongate-flexuose, strongly porose, smooth, yellow red; alar cells not differentiated. Setae elongate, smooth or at times papillose below the capsule. Capsules erect, ovoid, irregularly furrowed, wide-mouthed, constricted at neck; cells in neck isodiametric, very thick-walled, mammillose-bulging; stomata on capsule neck, deeply immersed; opercula obliquely long-rostrate; annuli rudimentary; peristome absent. Spores tetrahedral, trilete scar present. Calyptrae cucullate, smooth.

Rhacocarpus, a genus of seven species and three varieties, was revised by Frahm (1996). The genus is found mostly in the Southern Hemisphere. Bolivia, with four species, appears to be the center of distribution for *Rhacocarpus*. The genus is gametophytically characterized by the near absence of rhizoids, terminal perichaetia, stems that lack a central strand, and ecostate leaves with well-developed alar cells, distinct limbidia (except *R. chlorotus* Herzog), and peculiar leaf cell ornamentation that is absent from the perichaetial leaves. Sporophytically the genus is marked by elongate setae, ovoid to turbinate, furrowed capsules that lack a peristome and have deeply immersed stomata, obliquely long-rostrate opercula, and smooth, cucullate calyptrae. Its spores are also unusual in having a distinct trilete scar.

The rhizoids of *Rhacocarpus* are difficult to demonstrate since they are only found clustered at the base of what appear to be secondary stems; they do not occur at the base of branches. *Rhacocarpus* is not usually considered to have creeping primary stems, but the restricted position of rhizoids in this genus points to a primary/secondary stem system. The stem rhizoidal distribution in *Rhacocarpus* is similar to *Thamnobryum* (see Allen & Churchill 2002). It differs from the *Thamnobryum* system in that distinct creeping primary stems with rhizoids clustered at places where the stems touch the substrate are absent. *Rhacocarpus*, however, mostly occurs on rocks and possibly the absence of distinct creeping primary stems in this genus may be an artifact of careless collection technique such as has been discussed for *Fontinalis* (see Buck & Allen 1997).

Frahm (1996) attributed foliose pseudoparaphyllia to *Rhacocarpus*. These structures are rounded in shape, with sharply serrate margins and smooth leaf cells. They clearly occur at the base of branches or clustered on branch primordia, and, as noted by Buck (1995), are better considered "scaly leaves," *i.e.*, structures that protect the buds and are homologous to leaves (Akiyama & Nishimura 1993).

The Central American species of *Rhacocarpus* have distinctive leaf limbidia that result more from their usually deep red color and smooth surface rather than cell shape distinctions. The leaf border cells are narrower than the laminal cells, but there is a gradual transition from the median leaf cells to the border cells.

The oddest feature of *Rhacocarpus* is its leaf cell ornamentation. As shown by Delgadillo (1982)—see also Robinson 1971b; Barthlott and Schultze-Motel 1981; Buck 1995; Frahm 1996—the leaf cells in *Rhacocarpus* are prorate and covered by a perforate reticulum. Buck (1995) compared the perforate reticulum to pollen grain ornamentation; it also resembles some types of secondary peristomial ornamentation, see, *e.g.*, Allen (1980, fig. 25). Curiously, the perichaetial leaves of *Rhacocarpus* have prorate cells, but lack the perforate reticulum.

The name *Rhacocarpus* combines the Greek *rhaco* (ragged) and *carpos* (fruit). Lindberg (1862) used it in reference to the furrowed capsules of the genus.

1. Leaves with long, often hyaline hair-points . . . . . 2. *R. purpurascens*
1. Leaves with short to long, concolorous apicula. . . . . 1. *R. apiculatus*

1. *Rhacocarpus apiculatus* (Renauld & Cardot) Paris, Index Bryol. 1068. 1898. *Harrisonia apiculata* Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32(1): 174. 1894. Protologue. [Costa Rica] Forêts du Barba (*Pitt*[ier] *n^o^ 5613*).

Rhacocarpus squamosus R. S. Williams, Bull. New York Bot. Gard. 6(21): 237. 1909. Protologue. [Bolivia] Near Tolapampa, 3600 meters, Sept. 11, 1901 [*Williams*] (*2894*).

Plants medium-sized, in glaucous green, greenish yellow, or reddish yellow mats. Primary stems inconspicuous, creeping, sympodially branched, leaves reduced and distantly spaced; rhizoids rare, densely clustered at base of sympodial branches, red, smooth, more or less unbranched. Secondary stems prominent, prostrate or erect, irregularly branched from all sides of the stems; cross section with sclerodermis of 2–5 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow, thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, upper one oblong, lower one subquadrate, red. Secondary stem and branch leaves oblong to broadly elliptic, often panduriform, 1–2 mm long, erect to erect-spreading when dry, erect-spreading when wet, short to long apiculate, decurrent; margins narrowly recurved at base, broadly incurved above, serrulate; costa absent; cells linear-flexuose, 40–60 × 6 µm, thick-walled, porose, densely covered by a finely papillose reticulum; marginal cells longer, narrower, smooth, forming a distinct border; cells at the insertions smooth, linear, strongly porose, yellow to red; alar cells extensively developed, oblong to subquadrate, extremely thick-walled, porose, smooth. Dioicous. Perigonia gemmate, lateral on secondary stems and branches, 1–2 mm long. Perichaetia terminal, 3 mm long; leaves erect, elongate, cells elongate-flexuose, strongly porose, smooth to prorate from both ends, yellow red; alar cells not differentiated. Setae elongate, red, becoming blackish with age, 14–16 mm long, smooth below, densely papillose above. Capsules erect, ovoid, 2 mm long, irregularly furrowed, wide-mouthed, constricted at neck; exothecial cells small, red, thick-walled in several rows below the mouth, enlarged, irregularly long-rectangular below, moderately thin- to firm-walled in furrows, thick-walled on ridges; cells in neck isodiametric, extremely thick-walled, mammillose-bulging; stomata deeply immersed on neck; operculum not seen; annulus not seen; peristome absent. Spores tetrahedral, warty papillose on one side, with trilete scar on opposite side, 14–16 µm. Immature calyptrae cucullate, reddish brown, smooth, 3–4 mm long.

Illustrations. Frahm (1996, Fig. 4 b). Figure 11.

Habitat. On thin soil over rocks, on soil by streams, vertical, dripping cliffs; 2100–2700 m.

Distribution in Central America. COSTA RICA. Alajuela: *Griffin et al. 019999* (F, MO, NY); Heredia: *Crosby & Crosby 6552* (MO); Limón: *Davidse et al. 28849* (MO, NY); San José: *Standley 43609* (FH, NY).

World range: Central America; Western South America.

Rhacocarpus apiculatus has variably apiculate leaves, and this feature distinguishes it from the long, hair-pointed leaves of *R. purpurascens*. Nevertheless, the two species can at times be confused because the leaf hair-points in some collections of *R. purpurascens* are mostly detached. These collections, however, can be recognized as *R. purpurascens* by examining the stem and branch apical buds, which invariably have long, hair-pointed leaves. The apical buds of *R. apiculatus* have leaves with spreading, red apicula.

The leaves of *R. apiculatus* more closely resemble those of the Brazilian *R. inermis* (Müll. Hal.) Lindb. *in* Broth. than those of *R. purpurascens*. *Rhacocarpus inermis* differs from *Rhacocarpus apiculatus* in having broader, mucronate leaves with poorly differentiated borders, weakly serrulate margins, and thin-walled, mostly hyaline alar cells.

Frahm (1996) reported *R. apiculatus* from Bolivia based on the type of *R. squamosus*. A second Bolivian collection of this species is present in MO (*Lewis 83-709*). The date of publication for *Rhacocarpus squamosus* is usually given as 1910, the year in which the Bulletin of the New York Botanical Garden, volume 6 appeared. However, the paper in which the species was described was separately issued in October 1909.

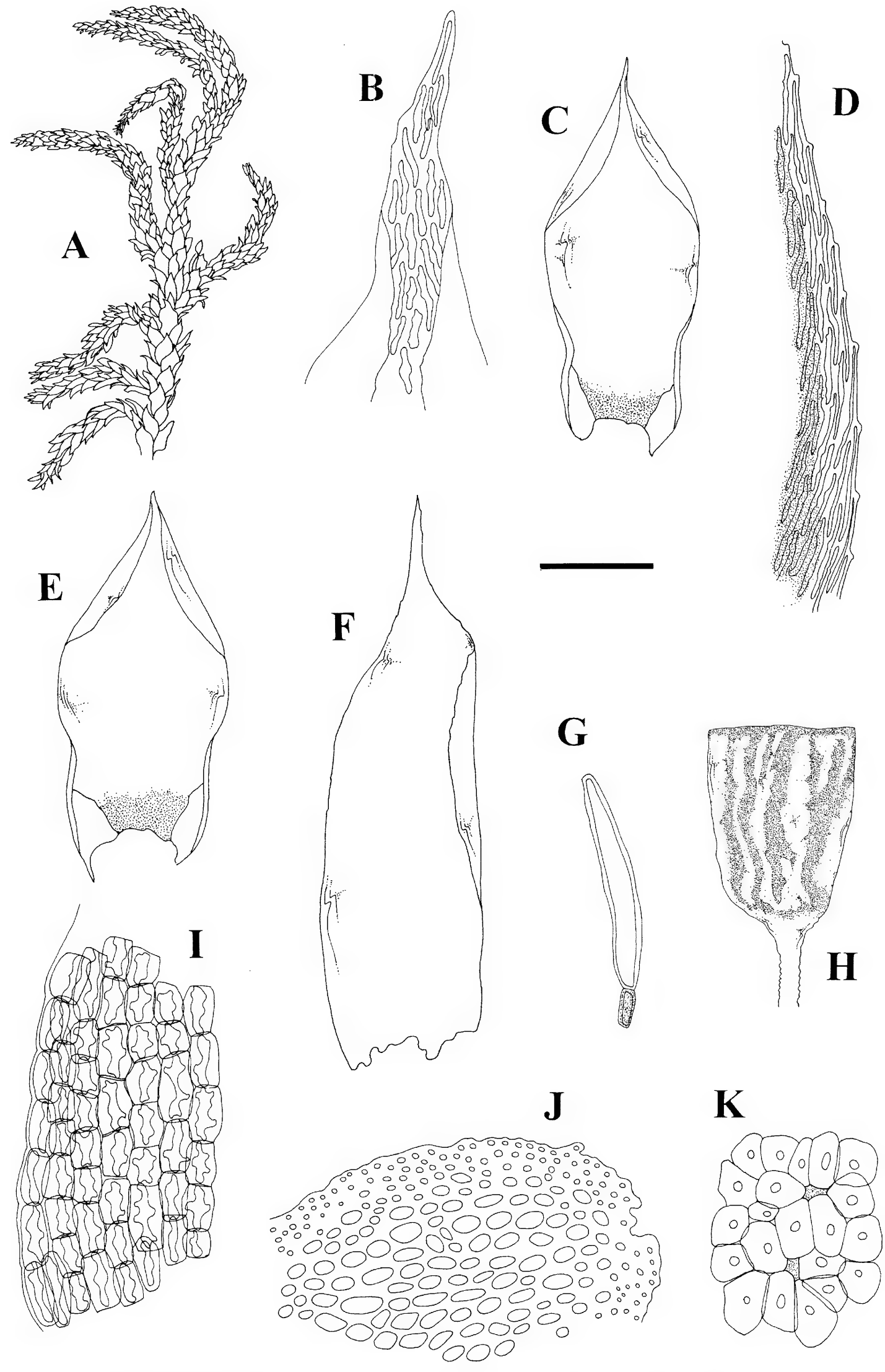
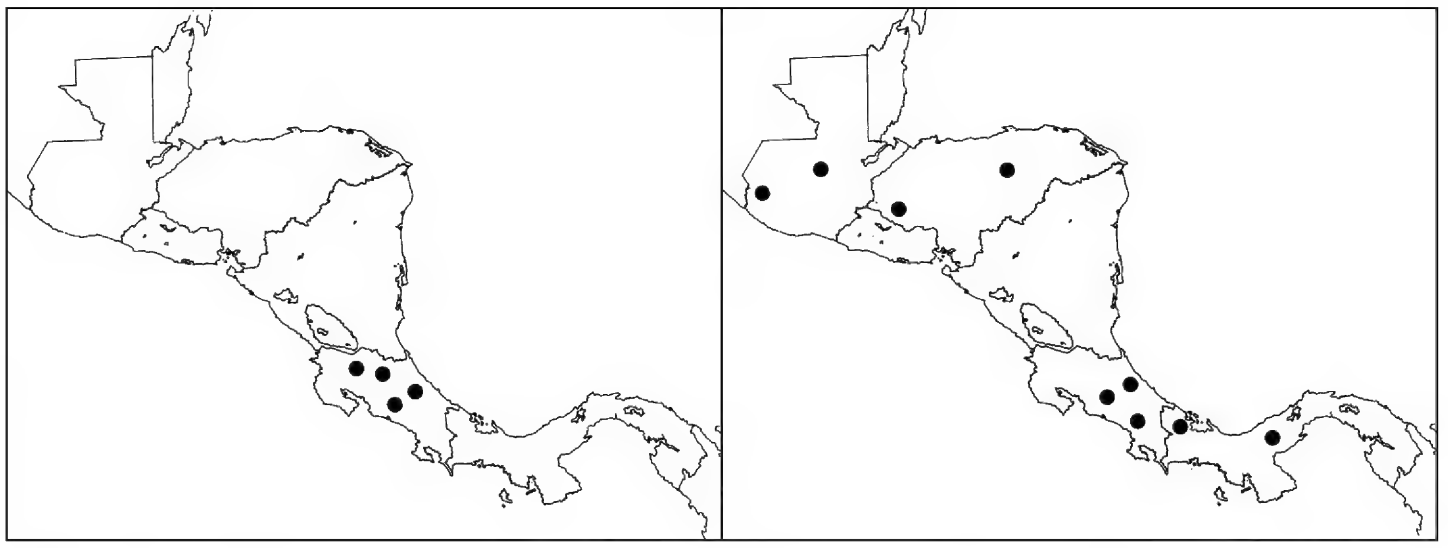


Figure 11. *Rhacocarpus apiculatus*. A. Habit. B. Leaf apex. C & E. Leaves. D. Leaf margins. F. Perichaetial leaf. G. Axillary hair. H. Seta and capsule. I. Alar cells. J. Stem in cross section. K. Exothecial cells showing two stomatal crypts. Scale in mm: bar = 0.06 (B, D, G, I, K); bar = 0.08 (J); bar = 0.34 (H); bar = 0.5 (C, E, F); bar = 4.0 (A). A–E, G, I from *Griffin 019999*; all other figure parts from *Davidse 28849*.



Rhacocarpus apiculatus *Rhacocarpus purpurascens*

2. *Rhacocarpus purpurascens* (Brid.) Müll. Hal., Oesterr. Bot. Z. 47: 392. 1897. *Hypnum purpurascens* Brid., Muscol. Recent. Suppl. 2: 121. 1812. Protologue. [Réunion] In caespitibus humentibus et ad saxa basaltica madida in Planitie des Chicots Insulae Borboniae hucusque tantum lectum est. *Clar. Bory St. Vincent* detexit et communicavit (type not present in B, Frahm 1996).

Anictangium humboldtii Hook., Pl. Crypt. Tab. 1 A. 1816. *Hedwigia humboldtii* (Hook.) Hook., Musci Exot. 2. Pl. 137. 1819. *Harrisonia humboldtii* (Hook.) Spreng., Syst. Veg. 4(1): 145. 1827. *Neckera humboldtii* (Hook.) Müll. Hal., Syn. Musc. Frond. 2: 102. 1850. Protologue. [Colombia] In monte Quindiu, locis frigidis, altit. 1580 hexapod, [*Humbold & Bonpland*].

Plants medium-sized, in glaucous green, greenish yellow, or reddish yellow mats. Primary stems inconspicuous, creeping, sympodially branched, leaves reduced; rhizoids rare, densely clustered at base of sympodial branches, red, smooth, more or less unbranched. Secondary stems prominent, prostrate or erect, irregularly branched from all sides of the stems; cross section with sclerodermis of 2–5 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow, thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, upper cell oblong yellowish hyaline, lower cell subquadrate, red. Secondary stem and branch leaves oblong to broadly elliptic, often panduriform, 1–2 mm long, erect to erect-spreading when dry, erect-spreading when wet, ending in a long, yellow, red, or hyaline hair-point, decurrent; margins narrowly recurved at base, broadly incurved above, serrulate; costa absent; cells linear-flexuose, 40–50 × 6 µm, thick-walled, porose, densely covered by a finely papillose reticulum; marginal cells longer, narrower, smooth, forming a distinct border; cells at the insertions smooth, linear, strongly porose, yellow to red; alar cells extensively developed, oblong to subquadrate, extremely thick-walled, porose, smooth. Dioicous. Perigonia gemmate, lateral on secondary stems and branches, 1–2 mm long. Perichaetia terminal, red, 3–5 mm long; leaves erect, elongate, very long hair-pointed, cells elongate-flexuose, strongly porose, smooth to prorate from both ends, yellow red; alar cells not differentiated. Sporophytes not seen in Central America, description based on plants from Mexico and Colombia. Setae elongate, dark red, 8–25 mm long, smooth below, lightly papillose below the capsule. Capsules erect, ovoid, 3 mm long, irregularly furrowed, wide-mouthed, constricted at neck; exothecial cells small, red, thick-walled in several rows below the mouth, enlarged, irregularly long-rectangular below, moderately firm-walled throughout; cells in neck isodiametric, extremely thick-walled, mammillose-bulging; stomata deeply immersed on neck; opercula obliquely long-rostrate, to 2 mm long; annuli rudimentary, reduced to a single-cell abscission layer; peristome absent. Spores tetrahedral, finely papillose on one side, with trilete scar on opposite side, 20–28 µm. Calyptrae cucullate, reddish brown, smooth, 3–4 mm long.

Illustrations. Hooker (1816, Tab. 1 A); Brotherus (1925, Fig. 486 A–H, as *R. australis*); Bartram (1949, Fig. 106 G); Sainsbury (1955, Fig. 1); Allison and Child (1971, p. 103); Scott and Stone (1976, Pl. 69); Koponen and Norris (1986, Fig. 12 a–d); Churchill and Linares (1995, Fig. 169 d–i); Sharp

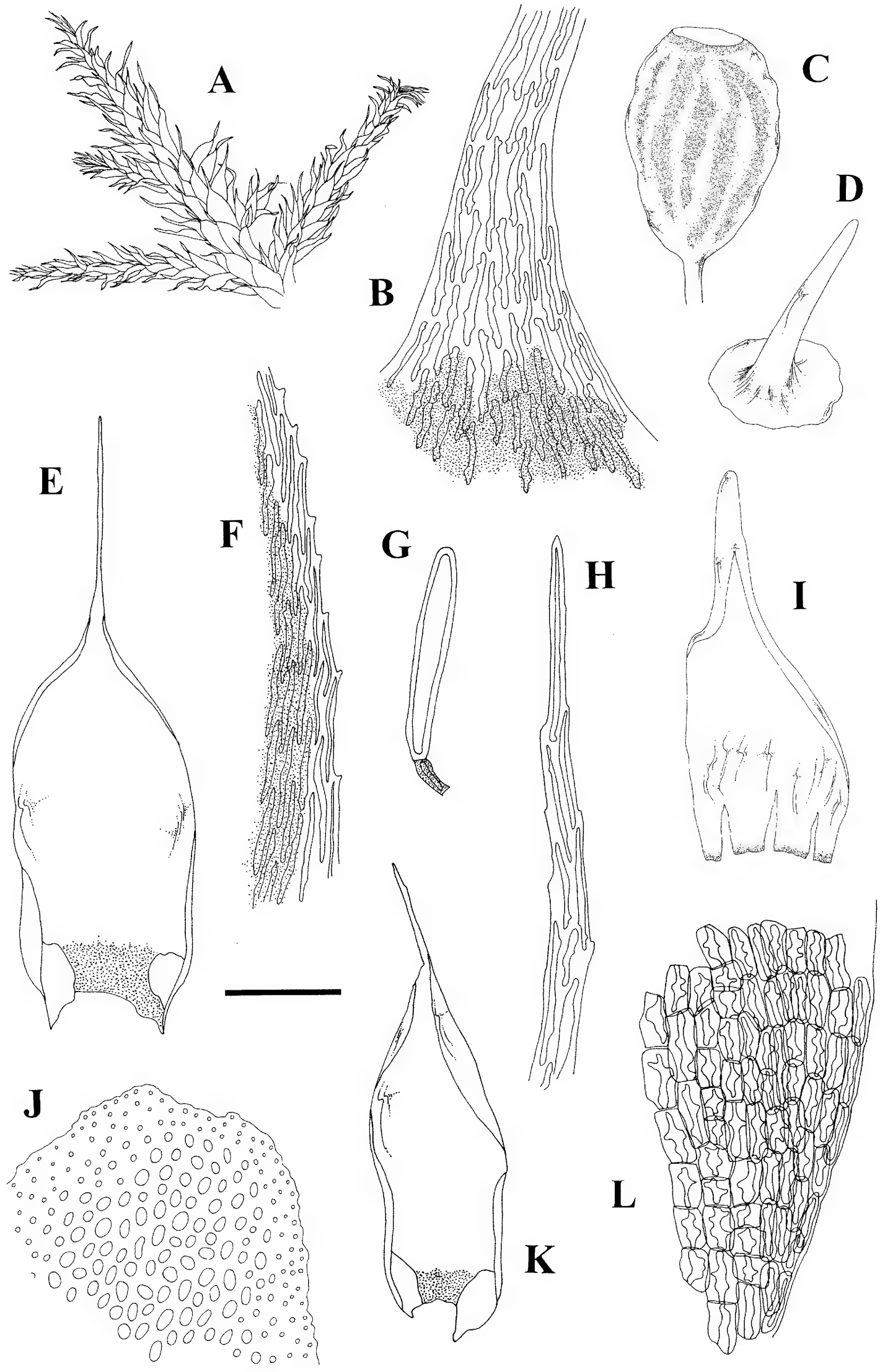


Figure 12. *Rhacocarpus purpurascens*. A. Habit. B. Leaf apex. C. Seta and capsule. D. Operculum. E & K. Leaves. F. Leaf margin. G. Axillary hair. H. Leaf tip. I. Calyptra. J. Stem in cross section. L. Alar cells. Scale in mm: bar = 0.06 (B, F, G, H, L); bar = 0.08 (J); bar = 0.5 (E, K); bar = 1.3 (C, D, I); bar = 3.2 (A). C, D, I from *Luteyn 7154*; all other figure parts from *Allen 11495*.

et al. (1994, Fig. 498); Magill and Rooy (1998, Fig. 151 1–11); Gradstein *et al.* (2001, Fig. 200 A–H). Figure 12.

Habitat. On humus over rocks and bare rocks, *Sphagnum* hummocks, wet banks, and epiphytic on shrubs: 1097–3600 m.

Distribution in Central America. GUATEMALA. Baja Verapaz: *Sharp 5236* (F, MO); San Marcos: *Steyermark 36449* (F, FH). HONDURAS. Lempira: *Allen 11495* (MO, NY, TEFH); Olancho: *Allen 12706* (MO, NY, TEFH). COSTA RICA. Limón: *Davidse et al. 26022C* (MO); Puntarenas: *Davidse et al. 23861* (MO, NY); San José: *Crosby 3898* (MO). PANAMA. Bocas del Toro: *Gómez et al. 22498* (MO, NY); Veraguas: *Hammel & Kress 8577* (MO, NY).

World range: Mexico; Central America; Caribbean; Western, Northern, and Southern, South America, Brazil; Subantarctic Islands; West Central and East Tropical Africa, Southern Africa, Western Indian Ocean; Malesia; Australia, New Zealand.

Rhacocarpus purpurascens is a widespread Southern Hemispheric species found at high elevations throughout Central America. It sometimes occurs mixed with *R. apiculatus*, which differs in having apiculate leaves, more strongly furrowed capsules, densely papillose setae, and warty spores. The two species are sometimes confused, because the sporophytes of *R. purpurascens* are not known from Central America (although some collections have both perigonia and perichaetia) and the leaves of *R. apiculatus* sometimes have extraordinarily long apicula. Furthermore, in some collections of *R. purpurascens* most of the leaves have detached hair-points. The two species can be reliably separated by examining the branch and stem buds. In *R. purpurascens* the branch and stem bud leaves are long hair-pointed, and often hyaline. The branch and stem bud leaves in *R. apiculatus* are apiculate, and often red in color.

CRYPHAEACEAE

Cryphaeaceae Schimp., Coroll. Bryol. Eur. 97. 1856.

Plants small, medium-sized, or large, in mats or pendent. Primary stems creeping, irregularly branched, rhizoids not or weakly branched, from circular cluster of initials at abaxial side of leaf insertions, sometimes extending onto base of costae. Secondary stems horizontal, erect or pendent, irregularly or pinnately branched; cross section with sclerodermis, enlarged cortical cells, central strand absent; paraphyllia absent; pseudoparaphyllia foliose or filamentous, at times with scale leaves. Leaves ovate, ovate-lanceolate, or lanceolate, acute or acuminate, decurrent; margins plane or revolute, entire, serrulate, or denticulate above; costae single, strong, occasionally spurred above, in cross section guide cells and stereid cells absent, of rounded, thick-walled, homogenous cells; cells smooth or prorate, thick-walled, oval, elliptic, rhombic, fusiform, elongate, or linear; basal cells near costa at base linear; alar cells rounded to subquadrate. Autoicous. Perigonia gemmate, lateral; perichaetia at the ends of short or long branches and at the ends of stems (*Schoenobryum*). Setae short, cells quadrate. Capsules immersed, ellipsoid, ovoid to oblong-ovoid, usually abruptly rounded-indented to the setae; stomata apparently absent or at capsule/seta junction; opercula conic, conic-mammillate, conic-apiculate, or short rostrate; annuli compound; peristome diplolepideous; exostome teeth narrowly triangular to linear; endostome when present with segments linear, cilia rudimentary or absent, basal membranes very low or absent. Spores spherical or irregularly oblong, at times massive. Spore germination exosporic or endosporic. Calyptrae mitrate or conic, smooth or prorate.

The Cryphaeaceae consist of nine genera: *Cryphaea* D. Mohr & F. Weber (31 species), *Cryphaeophilum* (Dusén) M. Fleisch. (1 species), *Cyptodon* (Broth.) Paris & Schimp. *ex* M. Fleisch. (4 species), *Cyptodontopsis* Dixon (1 species), *Dendrocryphaea* Broth. (7 species), *Dendropogonella* E. Britton (1 species), *Pilotrichopsis* Besch. (3 species), *Schoenobryum* Dozy & Molk. (16 species), and *Sphaerotheciella* M. Fleisch. (6 species). The family characteristically has creeping stolons with erect or pendent secondary stems that lack internal differentiation and paraphyllia, but usually have pseudoparaphyllia. Its rhizoids are nearly unbranched and generally come from circular clusters of initials at the abaxial side of the leaf insertion. The leaves are decurrent, and have strong single costae that lack internal differentiation and are sometimes spurred. Its leaf cells are thick-walled, and smooth or prorate. The leaf cells are typically short (although linear leaf cells occur in some taxa) and the basal cells in the alar region are usually quadrate to oblate. Members of the Cryphaeaceae are autoicous, and they have strongly differentiated perichaetial leaves, immersed capsules, reduced peristomes, and mitrate calyptrae. Significant generic variation within the family is found in habitat preference (epiphytes vs. rheophytes), habit (stems erect vs. pendent), perichaetial position (at the end of short vs. long branches), annulus form (compound and revoluble vs. absent), spore germination (exosporic vs. endosporic), and peristome form (endostome present vs. absent). Manuel (1982) provided an overview of the Cryphaeaceae.

Buck and Goffinet (2000) put *Dendroalsia* E. Britton into the Cryphaeaceae. The genus, however, is dioicous, and the presence of stem paraphyllia, emergent capsules, as well as cucullate calyptrae argues against placing it in the Cryphaeaceae.

1. Secondary stems and branches long and slender, pendent . . . . . 2. *Dendropogonella*
1. Secondary stems and branches short and rigid, erect 2

2. Sporophytes terminal on stems and branches. . . . . 3. *Schoenobryum*
2. Sporophytes lateral on stems and branches 3

3. Spores massive, 44–65 µm; germination endosporic; diaspores multicellular . . . . . 4. *Sphaerotheciella*
3. Spores medium-sized, 18–42 µm; germination exosporic; diaspores unicellular. . . . . 1. *Cryphaea*

Gametophytic key to the Central American species of
Cryphaea, *Schoenobryum*, and *Sphaerotheciella*

1. Stem leaf margins plane 2
1. Stem leaf margins revolute or recurved below 4

2. Leaf apices narrowly acute to broadly acuminate . . . . . *Schoenobryum julaceum*
2. Leaf apices acuminate to narrowly acuminate 3

3. Leaves ovate to ovate-lanceolate, apices gradually acuminate, occasionally twisted . . . . . *C. filiformis*
3. Leaves ovate to broadly ovate, apices abruptly acuminate, not twisted . . . . . *C. orizabae*

4. Leaves dimorphic: stem leaves lanceolate, costa 0.6–0.9 leaf length, margins weakly recurved, branch leaves ovate, costa 0.3–0.6 leaf length, margins mostly plane; all median leaf cells linear . . . . . *C. attenuata*
4. Stem and branch leaves differing only in size; median leaf cells away from the costa oval to elliptic 5

5. Leaves abruptly long-contracted above; costae 0.5–0.7 the leaf length 6
5. Leaves gradually narrowed above; costae 0.6–0.9 the leaf length 7

6. Leaf cells near the costa oblong or elliptic above midleaf . . . . . *C. apiculata* or *Schoenobryum rubricaule*
6. Leaf cells along costa narrowly elliptic to elongate above midleaf . . . . . *Sphaerotheciella gracillima*

7. Apical leaf margins entire to lightly scalloped . . . . . *Sphaerotheciella polycarpa*
7. Apical leaf margins serrulate, sharply serrate or coarsely denticulate 8

8. Leaves ovate-lanceolate to lanceolate; inner perichaetial leaf awns longer than leaf laminae . . . . . *C. jamesonii*
8. Leaves ovate to oblong-acuminate; inner perichaetial leaf awns shorter than leaf laminae 9

9. Upper leaf margins serrulate . . . . . *Schoenobryum concavifolium*
9. Upper leaf margins sharply serrate to coarsely denticulate 10

10. Costae 0.8–0.9 the leaf length, often distinctly wavy above, leaf cells from tip of costa to leaf apex elongate . . . . . *C. patens*
10. Costae 0.6–0.8 the leaf length, not wavy above, leaf cells from tip of costa to near the leaf apex elliptic . . . . . *Sphaerotheciella pinnata*

1. *Cryphaea* D. Mohr & F. Weber, Tab. Calyptr. Operc. 3. 1813 [1814]. *Pilotrichum* sect. *Cryphaea* (D. Mohr & F. Weber) Müll. Hal., Syn. Musc. Frond. 2: 163. 1851.

Neckera sect. *Cryphidium* Mitt., J. Linn. Soc., Bot. 12: 451. 1869. *Cryphidium* (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1874–75: 274. 1876.
Monocryphaea P. Rao, Bryobrothera 7: 105. 2001, *syn. nov.*

Plants small, medium-sized, or large, in green or yellow green or reddish green mats. Primary stems creeping, irregularly branched, secondary stems and branches at times transformed to primary stems at the tips; rhizoids red, smooth, not or weakly branched, from circular clusters of initials at abaxial side of leaf insertion and extending onto the costa base. Secondary stems horizontal or erect and loosely spreading, irregularly or pinnately branched; cross section with sclerodermis of 3–6 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, thick-walled cells, central strand absent; paraphyllia absent; pseudoparaphyllia foliose or filamentous and with scale leaves. Leaves monomorphic or dimorphic, ovate, ovate-lanceolate, or lanceolate, erect-patent, erect-imbricate, or imbricate when dry, erect, patent or wide-spreading when wet, acute or acuminate, apices sometimes twisted, variously decurrent; margins plane or revolute, entire, serrulate, or denticulate above; costae single, strong; cells smooth or prorate, thick-walled, upper cells elliptic, narrowly elliptic or linear, median cells elliptic or linear; basal cells near costa at base linear; alar cells rounded to subquadrate. Autoicous. Perichaetia lateral, leaves oblong to oblong-lanceolate, inner ones abruptly narrowed to long, smooth, papillose or spinose aristae, costa stoutly filling the apex, weakly developed at base and often absent at midleaf. Setae short, cells quadrate. Capsules immersed, ellipsoid, smooth, narrowed at the mouth, abruptly rounded-indented to the setae; exothecial cells small, red, in 2–3 rows below the mouth, irregularly short-rectangular below; stomata absent or rarely im-

mersed at base of capsule near seta; opercula conic, conic-mammillate, or conic-apiculate; annuli compound, often clinging to mouth after dehiscence; peristome diplolepideous, deeply inserted within the mouth; exostome teeth narrowly triangular, yellowish white, papillose or papillose above, smooth at base, free at tips or rarely united at the tips; endostome segments linear, papillose or smooth, cilia absent, basal membranes very low, at times endostome absent. Calyptrae mitrate, smooth or prorate.

Cryphaea is a genus of 31 species found mostly in the southern regions of the world. The genus is strictly corticolous (see Rao 2001) and often occurs in sparse turfs. The stolons in this genus are tightly appressed to the substrate, but its long secondary stems occur at more or less right angles to the stolons and project straight out from the substrate. The stolons in *Cryphaea* are so tightly appressed that unless the substrate is included in collections the specimens contain only secondary stems and branches. Rhizoids in *Cryphaea* occur primarily on the stolons and they can be very difficult to find or absent if the stolons are not collected. Nearly all *Cryphaea* species occasionally produce dense clusters of rhizoids from the lower dorsal surface of the costae. The leaves in *Cryphaea* are mostly erect-imbricate when dry, but all the species are remarkably hygroscopic and the leaves rapidly become wide-spreading when wet. The leaf cells in *Cryphaea* are thick-walled throughout, and nearly all the species have elongate inner basal leaf cells with quadrate cells in the alar regions.

Asexual structures are unknown in *Cryphaea* (Rao 2001), but due to its autoicous condition, sporophytes are common. The genus is fairly uniform in its sporophytic features with all species having immersed capsules and narrow exostome teeth. The endostome in *Cryphaea* is either very reduced (cilia absent, basal membranes very low to absent, segments linear) or absent. There are several taxonomically important features present in the perichaetial leaves, such as, relative awn length and whether the costae are present only at base, only in the apices, or are discontinuous. *Cryphaea* capsules are strongly rounded and indented near the area of setae attachment and this makes stomata difficult to observe. Although stomata have not been observed for most *Cryphaea* species, they still may be present in this difficult-to-evaluate region of the capsules.

The genus *Monocryphaea* has a single species (*M. ravenelii* (Austin) P. Rao) with capsules that lack an endostome and have the exostome teeth united at the tips. The genus is identical in all other ways to *Cryphaea*. Peristome reduction is common in *Cryphaea* (especially endostomial reduction), and without additional distinguishing features the recognition of this genus is unwarranted. *Cryphidium* differs from *Cryphaea* in having rounded leaf apices and very short, aristate inner perichaetial leaves. Buck (1980) also cited peristome ornamentation differences between the two genera: *Cryphidium* endostome smooth, exostome teeth smooth at base; *Cryphaea* exostome and endostome papillose. Rao (2001) recognized *Cryphidium* but at the same time included in *Cryphaea* a species (*C. ovalifolia* (Müll. Hal.) A. Jaeger) with obtuse leaves and shortly aristate (0.2 the length of the leaf) perichaetial leaves. Robinson (1972) considered the differences between the two genera unworthy of generic separation.

The genera *Cryphaea*, *Schoenobryum*, and *Sphaerotheciella* form a close group of mosses with nearly indistinguishable gametophytes. *Schoenobryum* differs from *Cryphaea* in having capsules at the ends of stems or long branches. All its species also have single (exostomial) peristomes. *Sphaerotheciella* differs from *Cryphaea* only in having somewhat broader capsules, large spores, and massive, endosporically germinated protonemata. If capsules or well-formed perichaetia are absent it is extremely difficult to distinguish *Cryphaea* from *Schoenobryum* and *Sphaerotheciella*. At the generic level *Schoenobryum* appears well founded by the combination of its sporophyte position and single peristome. The presence, however, in one *Cryphaea* species of a single peristome makes *Schoenobryum* considerably less distinct. Even more tenuous is the case for recognizing *Sphaerotheciella*. There is considerable overlap in capsule shape between *Cryphaea* and *Sphaerotheciella*, and it may be that endosporically germinated protonemata represent an environmentally induced feature. In this regard the genus *Leucodon* is especially noteworthy, because it occupies identical habitats and has species with either exosporically or endosporically germinated protonemata. In view of their very similar gametophytes, it might be better to treat *Cryphaea*, *Schoenobryum*, and *Sphaerotheciella* at the subgeneric rather than generic level.

The name *Cryphaea* is from the Greek *kryphaeos* (hidden) in reference to its immersed capsules.

1. Stem leaf margins plane 2
1. Stem leaf margins revolute to recurved below 3

2. Leaves ovate to ovate-lanceolate, apices gradually acuminate, occasionally twisted. . . . . 3. *C. filiformis*
2. Leaves ovate to broadly ovate, apices abruptly acuminate, not twisted . . . . . 5. *C. orizabae*

3. Leaves dimorphic: stem leaves lanceolate, costa 0.6–0.9 leaf length, margins weakly recurved, branch leaves ovate, costa 0.3–0.6 leaf length, margins mostly plane; all median leaf cells linear . . . . . 2. *C. attenuata*
3. Stem and branch leaves differing only in size; median leaf cells away from the costa oval to elliptic 4

4. Leaves abruptly long-contracted above; upper leaf margins entire; costae 0.5–0.7 the leaf length. . . . . 1. *C. apiculata*
4. Leaves gradually narrowed above; upper leaf margins sharply serrate to coarsely denticulate; costae 0.6–0.9 the leaf length 5

5. Leaves ovate-lanceolate to lanceolate, apices long-acuminate, often twisted; costae straight above; inner perichaetial leaf awns longer than laminae . . . . . 4. *C. jamesonii*
5. Leaves ovate to oblong-acuminate, apices acute to short-acuminate, not twisted; costae often wavy above; inner perichaetial leaf awns shorter than laminae . . . . . 6. *C. patens*

1. *Cryphaea apiculata* Schimp. *in* B.S.G., Bryol. Eur. 5: 35. 1850 (fasc. 44–45). Protologue. Professor Liebmann in Mexiko gesammelt und uns mitgetheilt. Type (see Manuel 1981). Mexico. Orizaba, 8000 ft. *Liebmann s.n.* (BM, lectotype; H, isolectotype).

Plants small, in green or yellow green mats. Primary stems creeping, irregularly branched, secondary stems and branches at times transformed to primary stems at the tips; stem-borne rhizoids not seen; rhizoids red, smooth, not or weakly branched, on the lower 1/3 dorsal surface of the costae. Secondary stems horizontal or erect and loosely spreading, to 5 cm long, irregularly or pinnately branched; cross section with sclerodermis of 3–6 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, thick-walled, central strand absent; paraphyllia absent; foliose pseudoparaphyllia and scale leaves present. Secondary stem and branch leaves ovate, 1–2 mm long, erect-imbricate when dry, wide-spreading when wet, abruptly short- to long-acuminate, shortly decurrent; margins revolute in lower 3/4 or less, entire, rarely serrulate above; costae strong, 0.5–0.7 the length of the leaves; cells smooth and thick-walled, upper cells elliptic to narrowly elliptic, 20–30 µm long, median cells elliptic, 9–15 µm long; basal cells near costa in lower 1/3 of leaf linear, 30–40 µm long; alar cells rounded to subquadrate, 8–14 µm. Autoicous. Perichaetia lateral, leaves oblong to oblong-lanceolate, inner ones abruptly narrowed to long, papillose to spinose aristae, less than 1/3 the leaf length, costae stoutly filling the apices, weakly developed at base and often absent at midleaf. Setae short, 0.1–0.2 µm long, yellow, cells quadrate. Capsules immersed, ellipsoid, 1.0–1.5 mm long, smooth, light brown, narrowed at the mouth, abruptly rounded-indented to the setae; exothecial cells small, red, in 2–3 rows below the mouth, irregularly short-rectangular below; stomata not seen; opercula conic, smooth, 0.5–0.6 mm long; annuli compound, often clinging to mouth after dehiscence; peristome diplolepideous, deeply inserted within the mouth; exostome teeth narrowly triangular, yellowish white, papillose, to 0.45 mm long; endostome segments linear, papillose, to 0.35 mm long, cilia absent, basal membranes very low. Spores spherical, papillose, 28–42 µm. Calyptrae mitrate, basally split, prorate, 0.6–0.7 mm long.

Illustrations. Manuel (1981, Fig. 3 a–h); Sharp *et al.* (1994, Fig. 515 f–g); Rao (2001, Fig. 17). Figure 13.

Habitat. On tree (*Carpinus*) bark; 1825–3491 m.

Distribution in Central America. GUATEMALA. Quetzaltenango: *Sharp 5037A* (TENN); Quiché: *Sharp 2374* (FH, MO, TENN, US); COSTA RICA. Cartago: *King C-1237* (US).

World range: Mexico; Central America; Western and Northern South America.

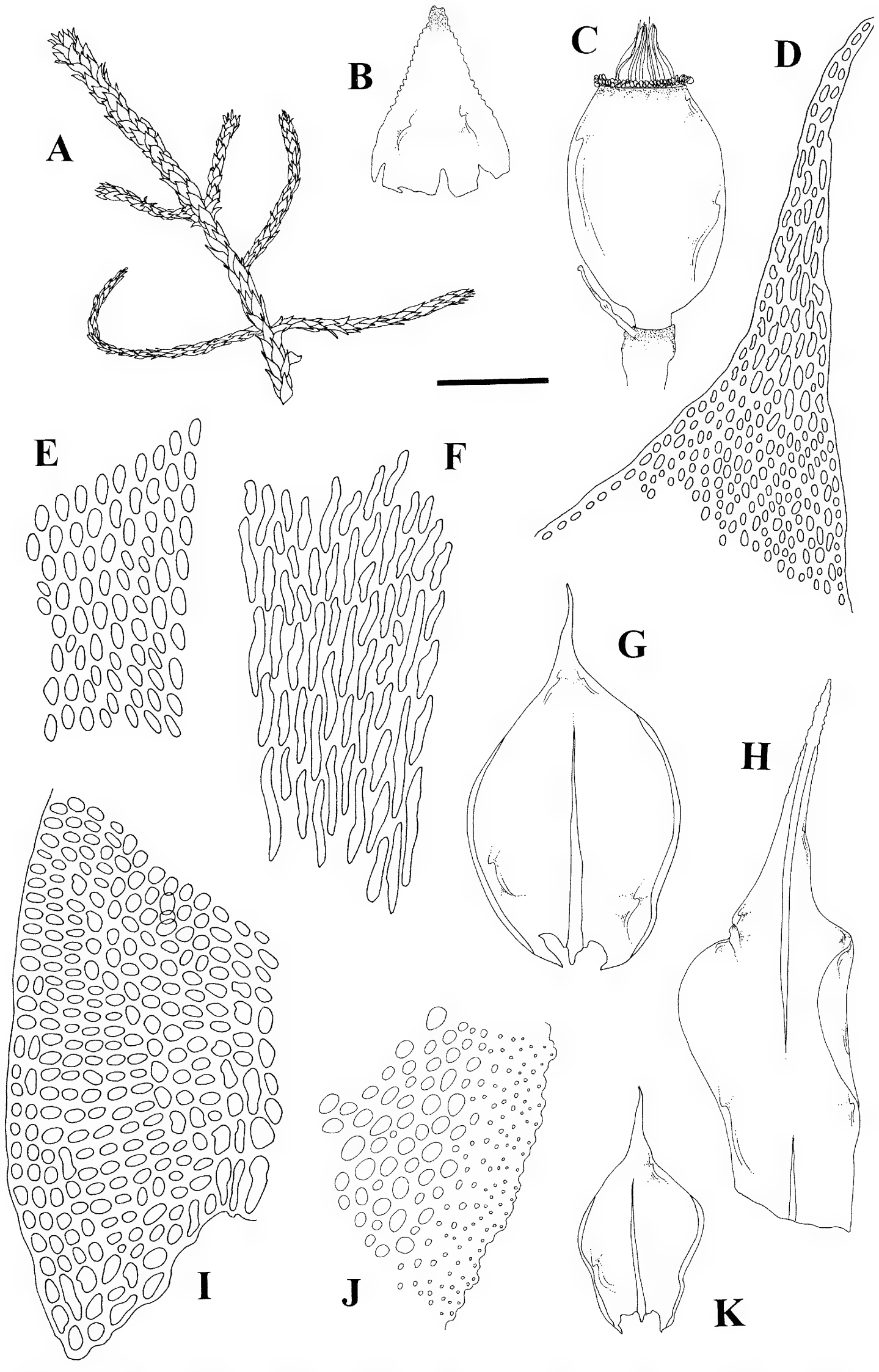
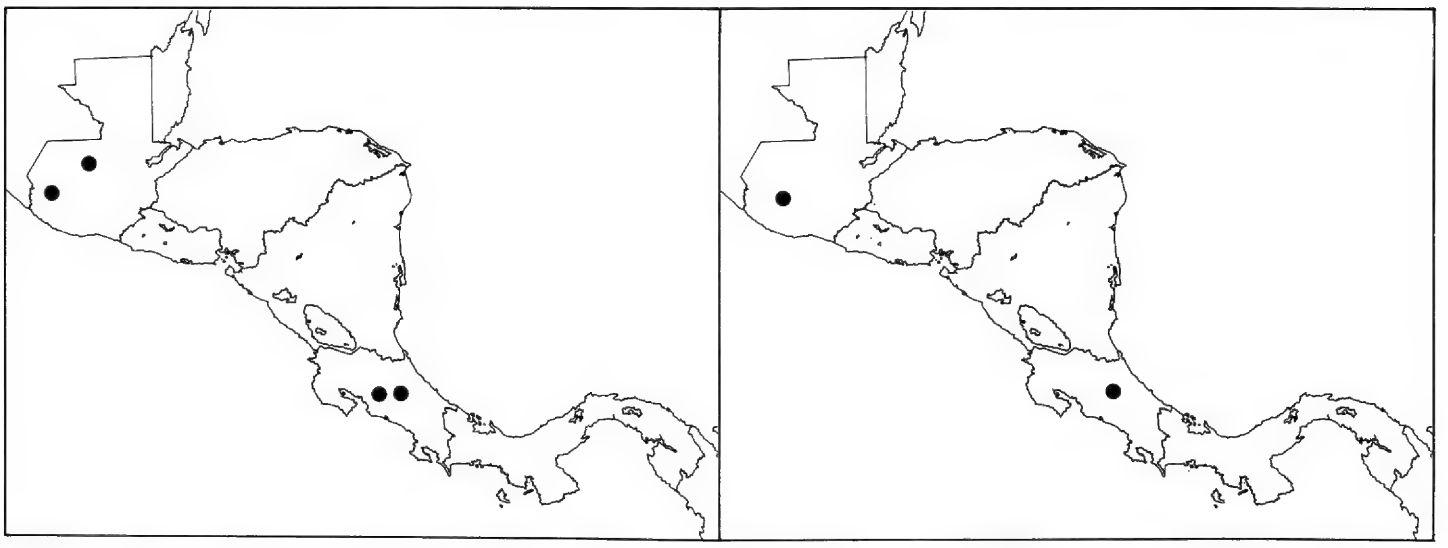


Figure 13. *Cryphaea apiculata*. A. Habit. B. Calyptra. C. Seta and capsule. D. Leaf apex. E. Median leaf cells. F. Basal median leaf cells. G. Stem leaf. H. Perichaetial leaf. I. Alar cells. J. Stem in cross section. K. Branch leaf. Scale in mm: bar = 0.05 (E, F, I); bar = 0.08 (J); bar = 0.1 (D); bar = 0.34 (B); bar = 0.6 (C, G, H, K); bar = 4.0 (A). All figure parts from *Sharp 2374*.



Cryphaea apiculata *Cryphaea attenuata*

Cryphaea apiculata has ovate leaves with recurved margins and short costae. Its leaves are abruptly contracted to slenderly acuminate tips, with entire or nearly so upper margins, and linear basal cells that are restricted to the lower one-third of the leaf. The leaves of *C. filiformis* and *C. orizabae* are similar in shape to those of *C. apiculata*, and all three species have short costae. The leaves of *C. filiformis* and *C. orizabae* differ from those of *C. apiculata* in having plane margins.

Schoenobryum concavifolium, *S. rubricaule*, and *Sphaerotheciella pachycarpa* also have ovate leaves with short costae, and when sporophytes are absent they can be confused with *C. apiculata*. The leaf apices in *Schoenobryum concavifolium* and *Sphaerotheciella pachycarpa* are acute to broadly acuminate, and this feature will separate them from *C. apiculata*. The leaves of *Schoenobryum rubricaule* are very similar to those of *C. apiculata*, and differ only in having more numerous thick-walled, elongate apical cells. *Sphaerotheciella pinnata* differs from *C. apiculata* in having ovate-lanceolate leaves with elongate cells in the central part of the leaves and multicellular spores. *Sphaerotheciella gracillima* can occasionally be confused with *C. apiculata* since both species have narrowly acuminate leaves. In *S. gracillima*, however, the leaves are more narrowly ovate below and its upper leaf cells are more elongate than those of *C. apiculata*.

2. *Cryphaea attenuata* Schimp. *in* B.S.G., Bryol. Eur. 5: 35. 1850 (fasc. 44–45). Protologue. Ebenfalls von *Prof. Liebmann* und früher von *Ehrenberg* aus Mexiko gebracht. Type (see Manuel 1981). Mexico. Chinantle, *Liebmann s.n.* (BM, lectotype).

Plants small, in green, yellow green, or reddish green mats. Primary stems creeping. Secondary stems horizontal or erect, pinnately branched, to 5 cm long; cross section with sclerodermis of 3–6 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia foliose and with scale leaves; rhizoids red, smooth, not or weakly branched, from circular clusters of initials at abaxial side of leaf insertions and extending onto the costae at the leaf bases. Leaves dimorphic; secondary stem leaves lanceolate, 1.6–2.2 mm long, erect-patent when dry, erect when wet, gradually and broadly acuminate, shortly decurrent; margins lightly recurved in lower 1/2, at times plane, entire to serrulate above; costae strong, 0.6–0.9 the leaf length; cells smooth and thick-walled, basal, median, and apical cells linear, 18–28 µm long, median cells 25–45 µm long; basal cells near costae to 95 µm long; alar cells rounded to subquadrate, 8–14 µm; branch leaves ovate, costae 0.3–0.6 the leaf length, margins nearly always plane. Autoicous. Perichaetia lateral, leaves oblong to oblong-lanceolate, inner ones abruptly narrowed to long, smooth to papillose aristae, more or less equal to leaf length, costae discontinuous, stoutly filling the apex, ending at midleaf. Setae short, 0.7–0.1 µm long, cells quadrate. Capsules immersed, ellipsoid, 1.7–2.0 mm long, smooth, light brown, narrowed at the mouth, abruptly rounded-indented to the setae; exothecial cells small, red, in 2–3 rows below the mouth, irregularly short-rectangular below; stomata immersed, at very base of capsule near seta; opercula conic, 0.4–0.6 mm long, smooth; annuli compound; peristome diplolepideous, deeply inserted within the mouth;

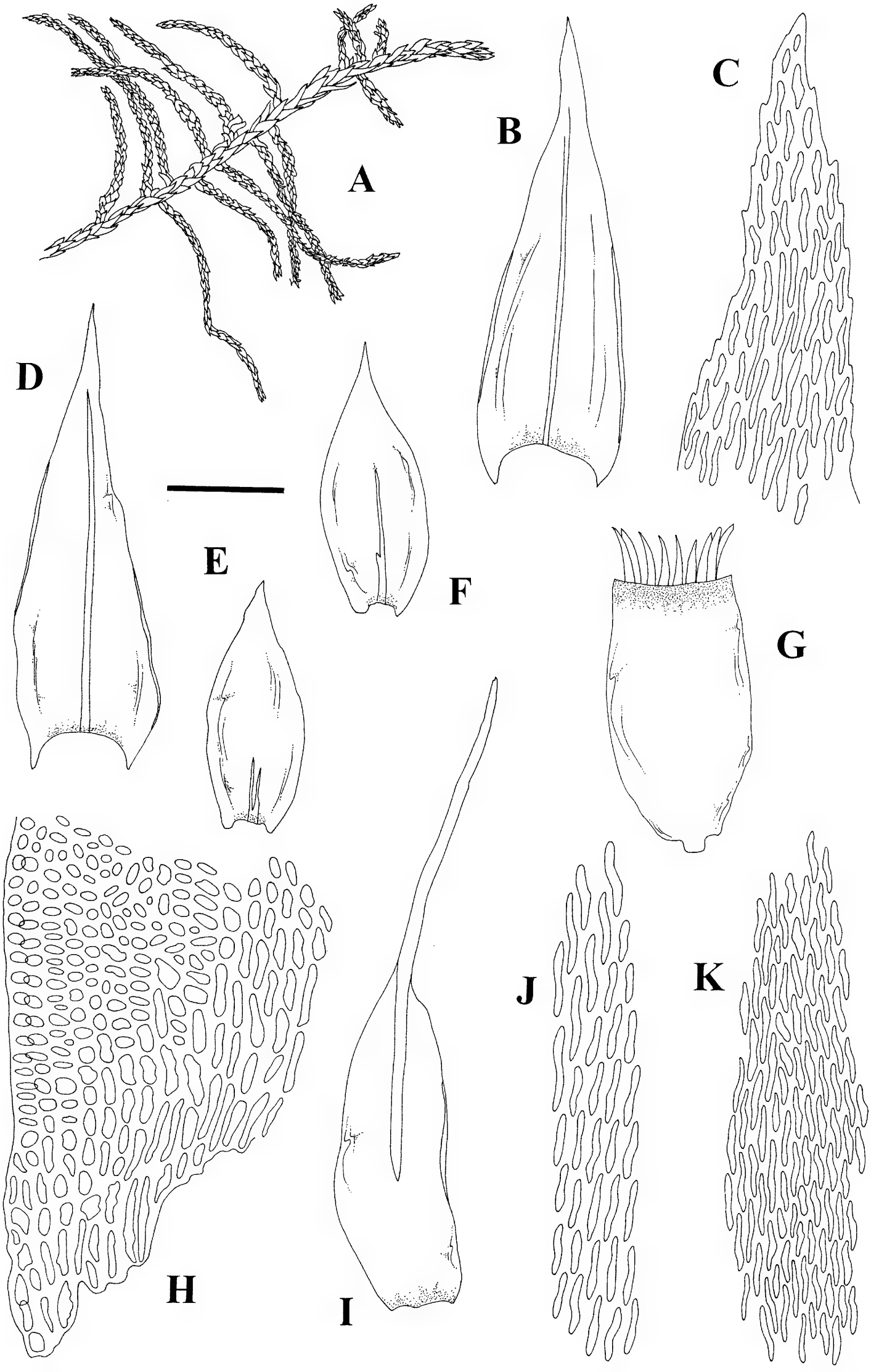


Figure 14. *Cryphaea attenuata*. A. Habit. B & D. Stem leaves. C. Leaf apex. E & F. Branch leaves. G. Seta and capsule. H. Alar region. I. Perichaetial leaf. J. Basal median leaf cells. K. Median leaf cells. Scale in mm: bar = 0.06 (C, H, J, K); bar = 0.5 (B, D–F, I); bar = 0.6 (G); bar = 5.1 (A). All figure parts from *Delgadillo 4793*.

exostome teeth narrowly triangular, hyaline to white, papillose, to 0.36 mm long; endostome segments linear, papillose, cilia absent, basal membranes very low. Spores spherical, papillose, 33–37 µm. Calyptrae mitrate, 0.4–0.6 mm long.

Illustrations. Manuel (1981, Fig. 3 i–o); Sharp *et al.* (1994, Fig. 515 c); Rao (2001, Fig. 18). Figure 14.

Habitat. On trees and shrubs; 2736 m.

Distribution in Central America. GUATEMALA. Chimaltenango/Sololá: *C. L. Gilly 148-e* (TENN). COSTA RICA. Cartago: *Crosby & Crosby 6174* (MO, TENN).

World range: Mexico; Central America.

Cryphaea attenuata is the only Central American species of *Cryphaea* with strongly dimorphic leaves: lanceolate stem leaves with long costae (0.6–0.9 the leaf length); ovate branch leaves with short costae (0.3–0.6 the leaf length). A more diagnostic feature of the species, however, is found in its leaf cells which are subquadrate in the alar regions, but otherwise linear. This areolation is so distinctive that collections without sporophytes can be difficult to assign to *Cryphaea*. The leaf areolation in *Sphaerotheciella gracillima* and *C. attenuata* is somewhat similar in that the former has linear or elongate cells near the costae, but its stem leaves are ovate-lanceolate rather than lanceolate, and its median cells are elliptic to oblong. Furthermore, *S. gracillima* has monomorphic leaves with strongly recurved margins, and its branch leaf costae extend into the leaf acumina. The leaf margins of *C. attenuata* are mostly plane, but occasionally they are weakly recurved and this can cause confusion with *C. filiformis*. *Cryphaea filiformis*, however, has monomorphic leaves with short, oval leaf cells. Manuel (1981) and Rao (2001) compared *Cryphaea attenuata* to *C. jamesonii*, but in the latter species the leaves have strongly recurved margins, coarsely denticulate apices that are often twisted when dry, and oval to oblong median leaf cells. Additionally, the branch leaves of *C. jamesonii* have long costae (0.6–0.9 the length of leaf).

The Costa Rican collection of *C. attenuata* cited by Manuel (1981, *Crosby & Crosby 6188* MO) is *S. gracillima*. The Guatemalan specimen of *Cryphaea attenuata* was collected by Charles L. Gilley and not A. J. Sharp as reported by Manuel (1981). This confusion was caused by the use of a template label on which the printed "A. J. Sharp" was not struck out.

3. *Cryphaea filiformis* (Hedw.) Brid., Muscol. Recent. Suppl. 4: 139. 1819 [1818]. *Neckera filiformis* Hedw., Sp. Musc. Frond. 202. 1801. *Pilotrichum filiforme* (Hedw.) P. Beauv., Prodr. Aethéogam. 83. 1805. *Daltonia filiformis* (Hedw.) Arn., Mém. Soc. Linn. Paris 5: 296. 1872. Protologue. Habitat in Hispaniola. [*Swartz*]. Type (see Manuel 1981). Hispaniola, *Swartz* (S, lectotype).

Plants small, in green or yellow green mats. Primary stems creeping, irregularly branched, secondary stems and branches at times transformed to primary stems at the tips; rhizoids red, smooth, not or weakly branched, from circular clusters of initials at abaxial side of leaf insertions and extending onto the costae at the leaf base. Secondary stems horizontal or erect and loosely spreading, to 6 cm long, irregularly branched; cross section with sclerodermis of 3–6 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, with very thick walls, central strand absent; paraphyllia absent; pseudoparaphyllia foliose and with scale leaves. Secondary stem and branch leaves ovate to ovate-lanceolate, 1–1.5 mm long, imbricate when dry, wide-spreading when wet, acuminate to gradually acuminate, shortly decurrent; margins plane, entire or somewhat crenulate above; costae strong, 0.5–0.7 the leaf length; cells smooth or prorate, thick-walled, upper cells elliptic to narrowly elliptic, 15–22 µm long, median cells elliptic, 11–18 µm long; basal cells near costa in lowermost part of leaf linear, 20–40 µm long; alar cells rounded to subquadrate, 8–14 µm. Autoicous. Perichaetia lateral, leaves oblong to oblong-lanceolate, inner ones abruptly narrowed to a long, papillose to spinose arista, aristae less than leaf length, costae stoutly filling the apex, weakly developed at base and often absent at midleaf. Setae short, 0.1–0.2 µm long, yellow, cells quadrate. Capsules immersed, ellipsoid, 1.0–1.5 mm long, smooth, light brown, narrowed at the mouth, abruptly rounded-indented to the setae; exothecial cells small, red, in 2–3 rows below the mouth, irregularly short-rectangular below; stomata not seen; opercula conic-apiculate, smooth, 0.5–0.6 mm long; annuli compound, often clinging to mouth after dehiscence; peristome diplolepideous, deeply inserted

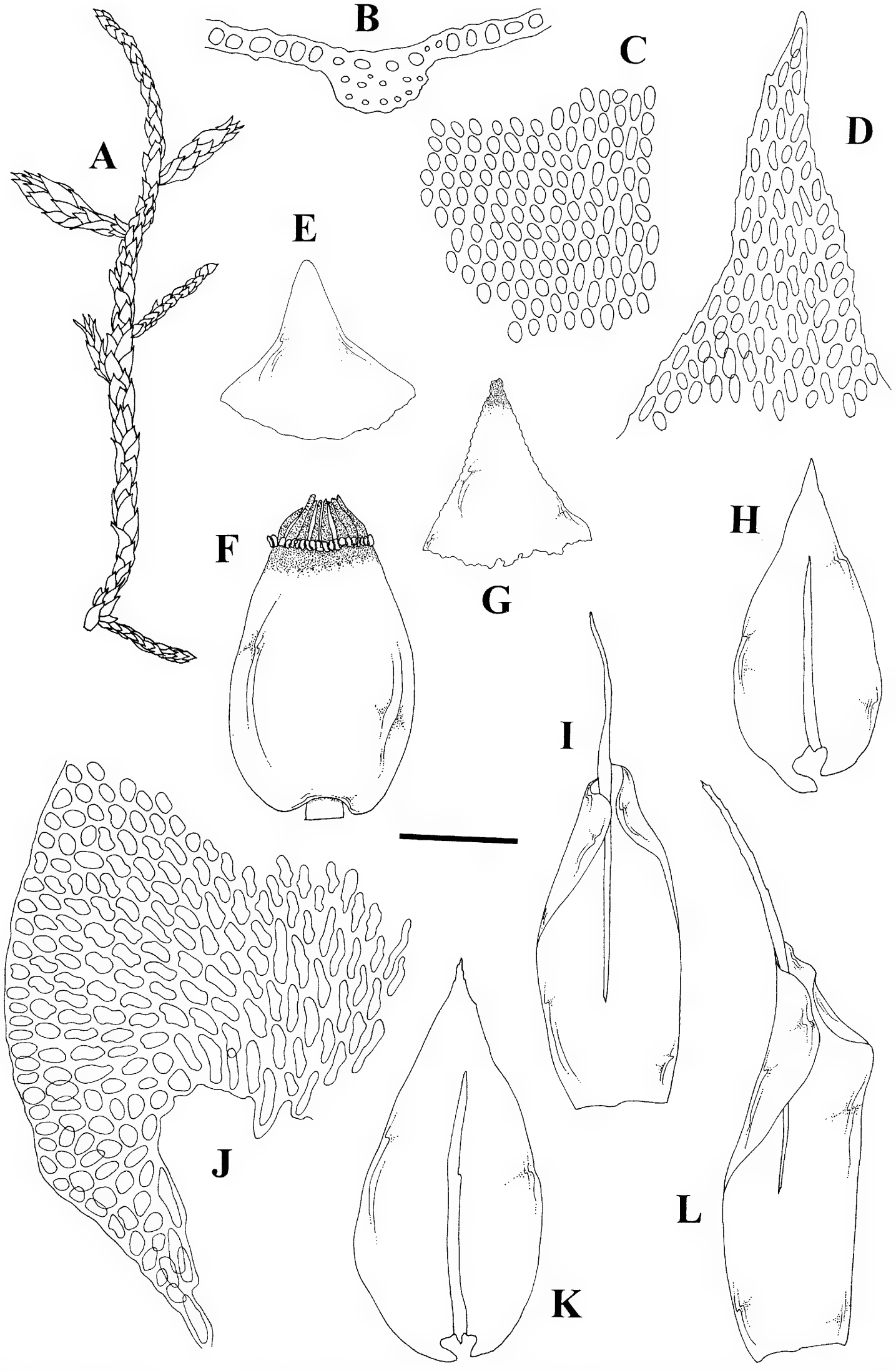
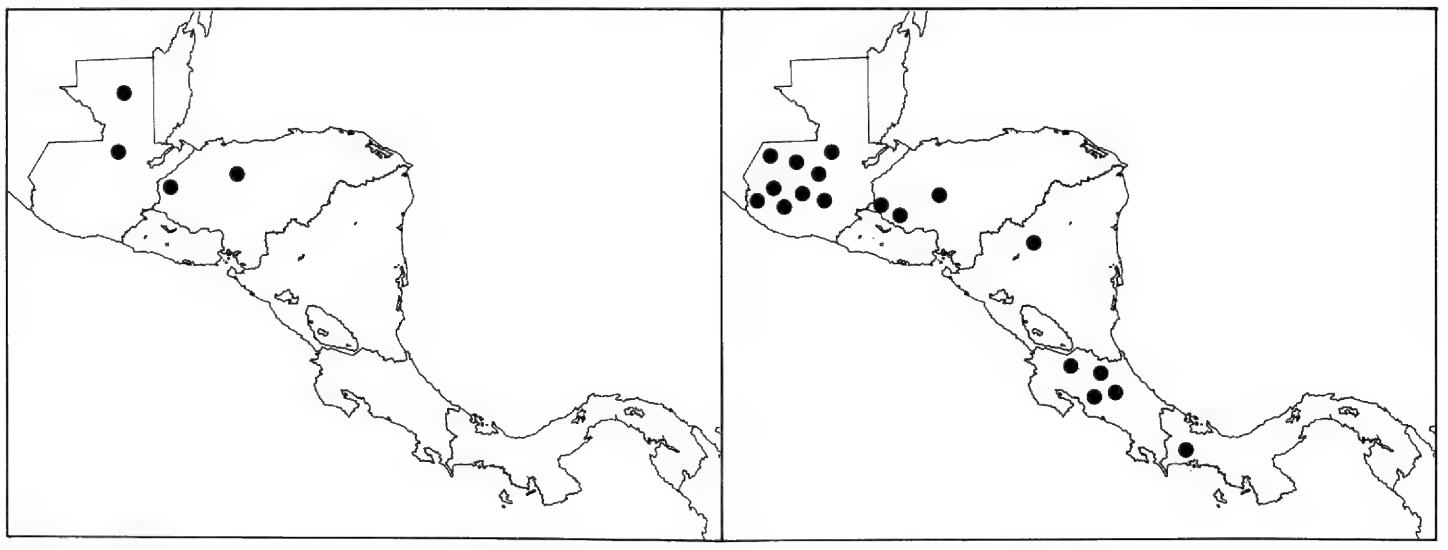


Figure 15. *Cryphaea filiformis*. A. Habit. B. Costa in cross section. C. Median leaf cells. D. Leaf apex. E. Operculum. F. Seta and capsule. G. Calyptra. H. Branch leaf. I & L. Perichaetial leaves. J. Alar region. K. Stem leaf. Scale in mm: bar = 0.06 (B, C, D, J); bar = 0.34 (E, G); bar = 0.5 (F, H, I, K, L); bar = 3.3 (A). All figure parts from *Pócs 578*.



Cryphaea filiformis *Cryphaea jamesonii*

within the mouth; exostome teeth narrowly triangular, yellowish white, papillose, to 0.4 mm long; endostome segments linear, papillose, to 0.35 mm long, cilia absent, basal membranes very low. Spores spherical, papillose, 18–28 µm. Calyptrae mitrate, basally split, prorate, 0.5–0.6 mm long.

Illustrations. Manuel (1973a, Fig. 4–7); Manuel (1981, Fig. 4 a–f); Crum and Anderson (1981, Fig. 357); Sharp *et al.* (1994, Fig. 514); Duarte Bello (1997, Pl. 174); Buck (1998, Pl. 64 1–8). Figure 15.

Habitat. Epiphytic; 200 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: *Standley 71789* (FH); Petén: *Lundell 2123a* (FH, MICH). HONDURAS. Copán: *Allen 17667A* (MO); Yoro: *Davidse 35496A* (MO).

World range: Southeastern U.S.A.; Mexico; Central America; Caribbean; Western and Southern South America, Brazil.

The ovate to ovate-lanceolate leaves of *Cryphaea filiformis* are tightly imbricate when dry, but strongly wide-spreading when wet. Its upper and median leaf cells are elliptic. The branch and stem leaf margins in *C. filiformis* are consistently plane, and this feature separates it from all other Central American *Cryphaea* species except *C. orizabae*. *Cryphaea orizabae* differs from *C. filiformis* in having most leaves abruptly contracted above rather than evenly and gradually narrowed to the apex. Several leaves should be examined when identifying the species because the leaves of *C. orizabae* are sometimes more or less gradually narrowed to the apex. The two species also differ in the width of their inner perichaetial leaves: *C. filiformis* 0.45–0.68 mm wide; *C. orizabae* 0.55–1.22 mm wide (Rao 2001).

Collections of *C. attenuata* are occasionally confused with *C. filiformis* because its branch leaf margins are mostly plane, and often the stem leaves have weakly recurved margins. *Cryphaea attenuata* consistently differs from *C. filiformis* in having dimorphic stem and branch leaves and elongate to linear rather than elliptic leaf cells. The leaves of *C. apiculata* and *C. filifomis* are similar in shape, and both species have short costae and an identical leaf areolation. The presence, however, of strongly recurved leaf margins on both its stem and branch leaves reliably separates *C. apiculata* from *C. filiformis*.

4. *Cryphaea jamesonii* Taylor, London J. Bot. 17: 192. 1848. Protologue. [Ecuador] On trees, on Pichincha. *Prof. W. Jameson*. Dec., 1846.

Cryphaea reticulata Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 213. 1872. Protologue. [Mexico] Orizaba (*Bourg*[*eau*] *n*^{o} *2763*, *pro parte*).

Cryphaea nitidula Schimp. *ex* Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 213. 1872. Protologue. [Mexico] Orizaba (*F. Müller*).

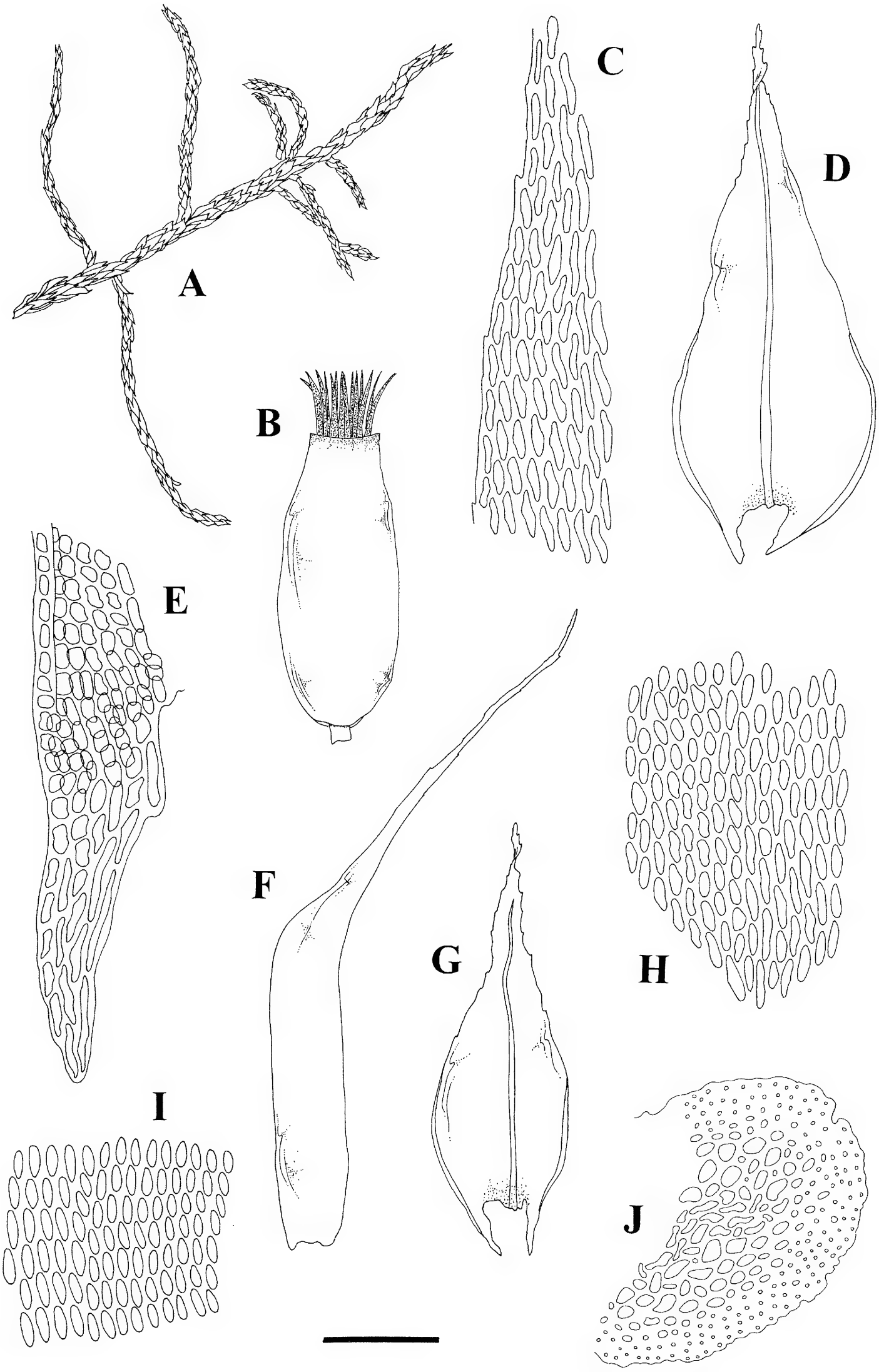


Figure 16. *Cryphaea jamesonii*. A. Habit. B. Seta and capsule. C. Branch leaf apical cells. D. Stem leaf. E. Alar region. F. Perichaetial leaf. G. Branch leaf. H. Branch leaf basal cells near costa. I. Median leaf cells. J. Stem in cross section. Scale in mm: bar = 0.06 (C, E, H, I); bar = 0.08 (J); bar = 0.5 (D, F, G); bar = 0.6 (B); bar = 5.1 (A). All figure parts from *Crosby & Crosby 6218*.

Plants medium-sized to large, in green or yellow green mats. Primary stems creeping, irregularly branched; rhizoids not seen. Secondary stems horizontal or erect and loosely spreading, to 7 cm long, irregularly or pinnately branched; cross section with sclerodermis of 3–6 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, very thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous and with scale leaves. Secondary stem and branch leaves ovate-lanceolate to lanceolate, 1.7–2.4 mm long, loosely imbricate, somewhat wrinkled when dry, patent when wet, gradually long-acuminate, apices often twisted, distinctly decurrent; margins revolute in lower 1/2, denticulate above; costa strong, 0.6–0.9 the leaf length; cells smooth and thick-walled, upper cells narrowly elliptic, 22–37 µm long, median cells elliptic, 11–18 µm long; basal cells near costa in lower 1/2 long elliptic, 14–22 µm long; alar cells rounded to subquadrate, 8–14 µm. Autoicous. Perichaetia lateral, leaves oblong to oblong-lanceolate, inner ones abruptly narrowed to long, serrulate to smooth aristae, as long as or more than the leaf length, costa stoutly filling the apex, weakly developed at base and often absent at midleaf. Setae short, 0.1–0.2 mm long, yellow, cells quadrate. Capsules immersed, narrowly ellipsoid, 1.2–2.0 mm long, smooth, light brown, narrowed at the mouth, abruptly rounded-indented to the setae; exothecial cells small, red, in 2–3 rows below the mouth, irregularly short-rectangular below; stomata immersed at base of capsule; opercula conic, smooth, 0.5–0.6 mm long; annuli compound, often clinging to mouth after dehiscence; peristome diplolepideous, inserted within the mouth; exostome teeth narrowly triangular, yellowish white, 0.4 mm long; endostome segments linear, papillose, 0.3 mm long, cilia absent, basal membranes very low. Spores spherical, papillose, 22–30 µm. Calyptrae mitrate, prorate, 0.4–0.6 mm long.

Illustrations. Bartram (1949, Fig. 108 D–F); Manuel (1981, Fig. 5 g–l); Sharp *et al.* (1994, Fig. 515 h–m); Churchill and Linares (1995, Fig. 52 e–h, not d); Buck (1998, Pl. 65 10–18); Magill and Rooy (1998, Fig. 153); Rao (2001, Fig. 25). Figure 16.

Habitat. On bark, trunks, branches, and twigs of shrubs and trees, and on logs; 1585–3109 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: *Standley 90368a* (F, FH); Baja Verapaz: *Sharp 2901* (FH, TENN); Chimaltenango: *Standley 61936a* (FH); Guatemala: *Standley 80654* (F, FH); Huehuetenango: *Sharp 4921a* (FH, TENN); Quetzaltenango: *Sharp 2266* (FH, TENN); Quiché: *Sharp 5308* (FH, TENN); San Marcos: *Sharp 5389* (FH, TENN); Sololá: *Kellerman s.n.* (US). HONDURAS. Comayagua: *Olson 84-31a* (MO); Lempira: *Allen 11436* (MO); Ocotepeque: *Allen 14424* (MO). NICARAGUA. Jinotega: *Crosby 2731A* (DUKE). COSTA RICA. Alajuela: *Standley & Torres 47878* (FH, US); Cartago: *Croat 35420A* (MO); Heredia: *Crosby & Crosby 6466* (MO); San José: *Crosby & Crosby 6218* (MO). PANAMA. Chiriquí: *Allen 9156A* (MO).

World range: Mexico; Central America; Caribbean; Northern and Western South America, Brazil; West Central and East Tropical Africa, South Africa, Western Indian Ocean.

Cryphaea jamesonii is the most common species of *Cryphaea* in Central America. It has long-acuminate leaves that are often twisted at the apex and somewhat wrinkled when dry. These features give it an aspect not seen in most other *Cryphaea* species, which have leaves smoothly imbricate when dry. This species can often be recognized with a hand lens due to its strongly spreading, very long, aristate inner perichaetial leaves. *Cryphaea attenuata* is the only other Central American species with similar inner perichaetial leaves, but its perichaetial leaves are more or less erect and its branches are mostly imbricate when dry.

Microscopically, *C. jamesonii* is distinguished by its gradually long-acuminate leaves with strongly recurved, denticulate margins. Other distinctive features of *C. jamesonii* include its decurrent leaves, nearly percurrent costae, and mostly narrow-elliptic leaf cells. *Cryphaea jamesonii* also differs from most other Central America *Cryphaea* species, in having filamentous pseudoparaphyllia (present also in *C. orizabae*) and immersed stomata (present also in *C. attenuata*).

5. *Cryphaea orizabae* Schimp. *ex* Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 214. 1872. Protologue. [Mexico] Orizaba (*Lorentz* comm.).

Plants small to medium-sized, in green or yellow green mats. Primary stems creeping, irregularly branched; rhizoids red, smooth, not branched, from circular clusters of initials at abaxial side of leaf insertion and extending onto the costae at the leaf bases. Secondary stems horizontal or erect and

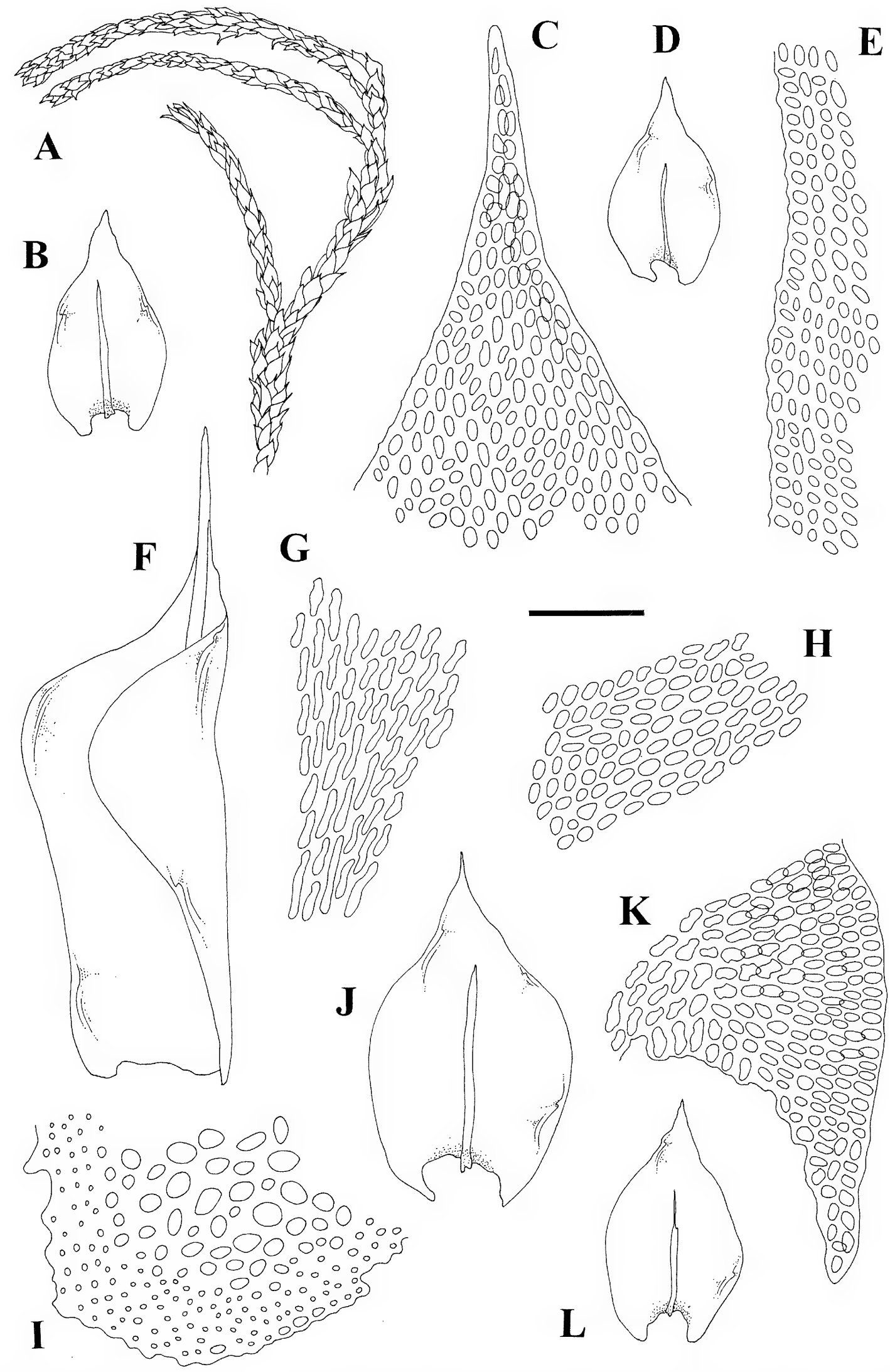
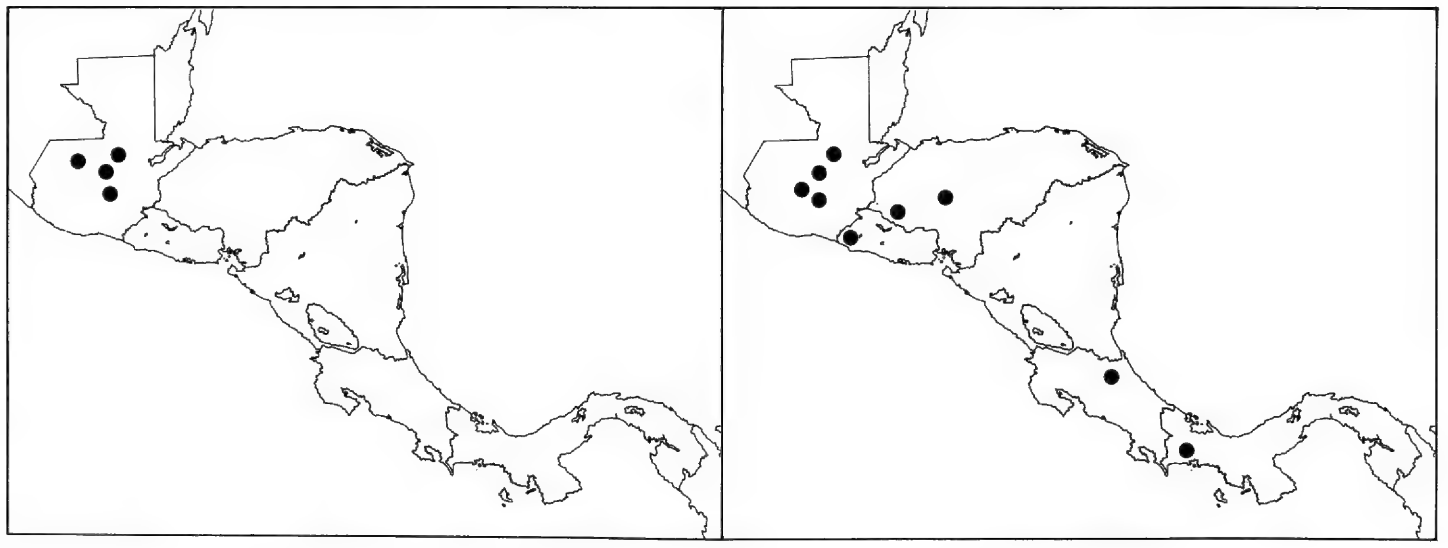


Figure 17. *Cryphaea orizabae*. A. Habit. B, D & L. Branch leaves. C. Leaf apex. E. Upper leaf margin. F. Perichaetial leaf. G. Lower leaf cells along costa. H. Median leaf cells. I. Stem in cross section. J. Stem leaf. K. Alar region. Scale in mm: bar = 0.06 (C, E, G, H, I, K); bar = 0.5 (B, D, F, J, L); bar = 0.6 (B); bar = 2.6 (A). All figure parts from *Sharp 2346A*.



Cryphaea orizabae *Cryphaea patens*

loosely spreading, to 6 cm long, irregularly branched; cross section with sclerodermis of 3–6 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, very thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia foliose and/or filamentous and with scale leaves. Secondary stem and branch leaves ovate-lanceolate, 1–1.5 mm long, imbricate when dry, wide-spreading when wet, slightly contracted to short acumina, shortly decurrent; margins plane, entire or somewhat crenulate above; costae strong, 0.5–0.7 the leaf length; cells smooth or prorate, thick-walled, upper cells narrowly elliptic to elliptic, 13–22 µm long, median cells elliptic, 11–22 µm long; basal cells near costae in lowermost part of leaf linear, 20–40 µm long; alar cells rounded to subquadrate, 8–14 µm. Autoicous. Perichaetia lateral, leaves oblong to oblong-lanceolate, inner ones with wide shoulders, abruptly narrowed to long, papillose to spinose aristae, aristae 0.3–0.5 the leaf length, costae stoutly filling the apex, weakly developed at base and often absent at midleaf. Setae short, 0.1–0.2 µm long, yellow, cells quadrate. Capsules immersed, ellipsoid, 1.3–1.7 mm long, smooth, light brown, narrowed at the mouth, abruptly rounded-indented to the setae; exothecial cells small, red, in 2–3 rows below the mouth, thin-walled, irregularly short-rectangular below; stomata not seen; operecula conic-apiculate, smooth, 0.5–0.6 mm long; annuli compound, often clinging to mouth after dehiscence; peristome diplolepideous; exostome teeth narrowly triangular, yellowish white, papillose, to 0.4 mm long; endostome segments linear, papillose, to 0.35 mm long, cilia absent, basal membranes very low. Spores spherical, papillose, 20–35 µm. Calyptrae mitrate, basally split, prorate, 0.5–0.6 mm long.

Illustrations. Bartram (1949, Fig. 107 G–I, as *Cryphaea pinnata*); Manuel (1981, Fig. 4 g–l); Sharp *et al.* (1994, Fig. 515 a–b); Rao (2001, Fig. 27). Figure 17.

Habitat. On bark, trunks, and branches of trees and shrubs (*Carpinus*), and on rotting branches; 300–2134 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: *Standley 69556a* (F, FH); Baja Verapaz: *Geissler s.n.* (G); Guatemala: *Svihla 2803* (FH); Quiché: *Sharp 2473* (FH, TENN, US).

World range: Mexico; Central America; Caribbean; Brazil.

Cryphaea orizabae and *C. filiformis* are the only Central American species of *Cryphaea* with plane leaf margins. The two species are very similar, especially in habit, and I doubt they can be distinguished in the field. *Cryphaea filiformis* differs from *C. orizabae* in having leaves that are evenly and gradually narrowed to the apex. Those of *C. orizabae* are variously contracted from midleaf to the apex. Since some leaves of *C. orizabae* can be more or less gradually narrowed to the apex, it is important to examine several leaves in order to make a proper identification. As noted by Rao (2001) the two species also differ in the width of their inner perichaetial leaves: *C. filiformis* 0.45–0.68 mm wide; *C. orizabae* 0.55–1.22 mm wide. Manuel (1981) pointed out that Bartram's (1949) concept of *Cryphaea pinnata* referred to *C. orizabae* and not *Cryphaea pinnata* (= *Sphaerotheciella pinnata*).

6. *Cryphaea patens* Hornsch. *ex* Müll. Hal., Linnaea 18: 679. 1845. Protologue. Mexico: *C. Ehrenberg*. Hb. Schlechtend[al].

Cryphaea intermedia Müll. Hal., Linnaea 19: 212. 1846. Protologue. Hab. in Mexico ubi retulit *Leibold*. Inter *Cryphaceam Leiboldi* et *filiformem* crescentem communicavit cl. *Gottsche*.

Cryphaea polycarpa Schimp. *ex* Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 215. 1872. Protologue. [Mexico] Cordova (*F. Müller*).

Cryphaea sartorii Schimp. *ex* Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 216. 1872. Protologue. [Mexico] Orizaba. (*F. Müller*).

Plants medium-sized, in green or yellow green mats. Primary stems creeping, irregularly branched; rhizoids from clusters of initials at the abaxial side of the leaf insertions, red, smooth, unbranched or rarely irregularly branched. Secondary stems horizontal or erect and loosely spreading, to 6 cm long, irregularly or pinnately branched; cross section with sclerodermis of 3–6 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, very thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous or subfoliose and with scale leaves. Secondary stem and branch leaves ovate, 1–2 mm long, erect-imbricate when dry, wide-spreading when wet, acute to somewhat acuminate, decurrent; margins revolute in lower 3/4 or less, crenulate to denticulate above; costae strong, 0.8–0.9 the leaf length, often wavy above; cells smooth, thick-walled, upper cells elliptic, 10–15 µm long, cells from tip of costa to leaf apex elongate, to 22 µm long, median cells round to elliptic, 6–15 µm long; basal cells near costa in lower 1/6 of leaf elongate to linear, 20–35 µm long; alar cells rounded to subquadrate, 6–12 µm. Autoicous. Perichaetia lateral, leaves oblong to oblong-lanceolate, inner ones abruptly narrowed to long, papillose to spinose aristae, 1/2 or less the leaf length, costa stoutly filling the apex, weakly developed at base and often absent at midleaf. Setae short, 0.1–0.2 µm long, red, cells quadrate. Capsules immersed, ellipsoid, 1.0–1.5 mm long, smooth, light brown, narrowed at the mouth, abruptly rounded-indented to the setae; exothecial cells small, red, in 2–3 rows below the mouth, thin-walled, irregularly short-rectangular below; stomata absent; opercula conic-mammillate, smooth, 0.5 mm long; annuli compound, often clinging to mouth after dehiscence; peristome diplolepideous, deeply inserted within the mouth; exostome teeth narrowly triangular to linear, white, 0.35–0.40 mm long; endostome segments linear, papillose, shorter than the exostome, cilia absent, basal membranes very low. Spores spherical or irregularly oblong, lightly papillose, 28–34 µm. Calyptrae mitrate, smooth to lightly prorate, 0.5 mm long.

Illustrations. Manuel (1981, Fig. 5 a–f); Sharp *et al.* (1994, Fig. 515 d–e); Churchill and Linares (1995, Fig. 52 a–c); Buck (1998, Pl. 65 10–18); Rao (2001, Fig. 28). Figure 18.

Habitat. On bark of tree trunks, shrubs, and branches, also on rotting logs; 500–2000 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: *Türckheim 6654* (FH); Baja Verapaz: *Sharp 2838* (TENN, mixed and filed with *C. jamesonii*); Chimaltenango: *Standley 81074* (FH); Sacatepéquez: *Standley 58873* (FH). EL SALVADOR. Ahuachapán: *Standley & Padilla 2696* (FH). HONDURAS. Comayagua: *Allen 13698B* (MO); Lempira: *Allen 11848* (MO). COSTA RICA. Heredia: *Crosby 9893* (MO). PANAMA. Chiriquí: *Allen 9067D* (MO).

World range: Mexico; Central America; Caribbean; North, Western, and Southern South America, Brazil.

Cryphaea patens is a fairly common species in Central America. It differs from the other Central American species of *Cryphaea* in having ovate leaves with recurved margins and gradually narrowed, crenulate to denticulate apices. *Cryphaea jamesonii* and *C. patens* are similar in having sharply serrate to coarsely denticulate upper leaf margins and long costae. However, *C. jamesonii* has long-acuminate leaves that are somewhat wrinkled when dry and this gives it an aspect very different from the smoothly imbricate leaves of *C. patens*. It further differs from *C. patens* in having strongly spreading, very long-aristate inner perichaetial leaves.

The gametophytes of *C. patens* are extremely difficult to separate from *Sphaerotheciella pinnata*. When sporophytes are present the two species can technically be distinguished, since the spores of *C. patens* are unicellular while those of *S. pinnata* are multicellular. The mature capsules of *S. pinnata*, however, rarely contain spores and even at the time of capsule maturation its spores (although huge in size) are unicellular. Gametophytically the two species are identical in habit, as well as leaf

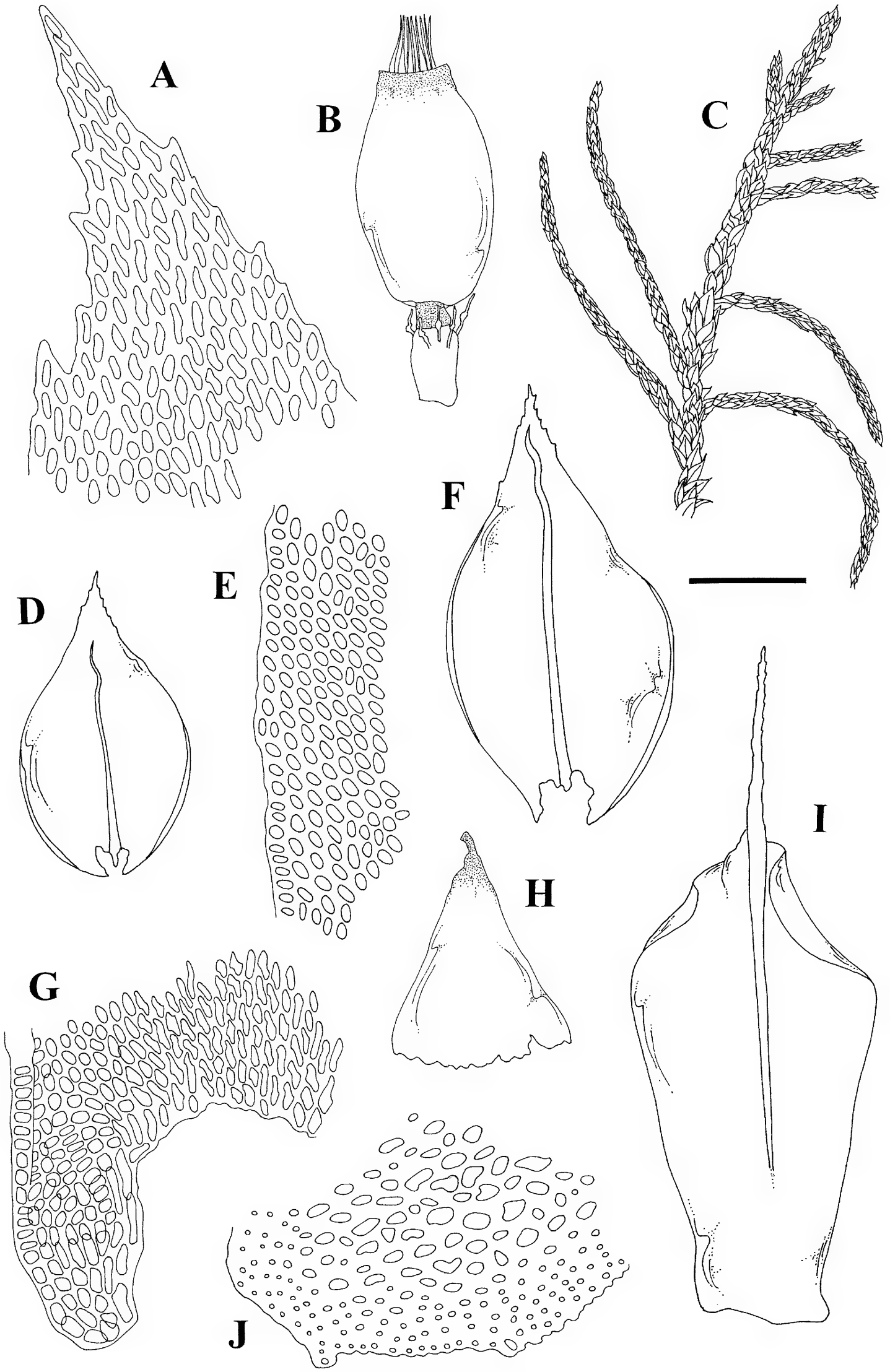


Figure 18. *Cryphaea patens*. A. Leaf apex. B. Seta and capsule. C. Habit. D. Branch leaf. E. Leaf margin. F. Stem leaf. G. Alar region. H. Calyptra. I. Perichaetial leaf. J. Stem in cross section. Scale in mm: bar = 0.06 (A, E, G, J); bar = 0.26 (H); bar = 0.41 (D, F, I); bar = 0.6 (B); bar = 4.0 (C). All figure parts from *Allen 13698B*.

shape, marginal denticulation, and apex form. The leaves of *S. pinnata* differ from those of *C. patens* in having much shorter, straight costae and oval to elliptic leaf cells from the tips of costae to near the leaf apices. In contrast, the costae of *C. patens* end very near the leaf apices and are often wavy above, and the leaf cells from the tip of the costae to the apices are elongate.

2. *Dendropogonella* E. Britton, Bryologist 9: 39. 1906. New name for *Dendropogon* Schimp., Bot. Zeitung (Berlin) 1: 377. 1843, illegitimate homonym. Not *Dendropogon* Raf., 1824. *Cryphaea* sect. *Dendropogon* (Schimp.) Müll. Hal., Linnaea 18: 682. 1844 [1845]. *Pilotrichum* sect. *Cryphaea* subsect. *Dendropogon* (Schimp.) Müll. Hal., Syn. Musc. Frond. 2: 173. 1851.

Plants slender, pendent in reddish brown to dull red festoons, yellow green at tips of stems and branches. Stems flexuose, slender, irregularly pinnately branched; cross section with sclerodermis of several rows of very small, red brown, thick-walled cells, cortical cells enlarged, yellow, thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia foliose; rhizoids rarely seen, on parts of stems that touch the substrate, red, short, smooth, not or rarely branched, from clusters of initials, abaxial to the leaf insertions. Stem and branch leaves narrowly lanceolate, imbricate to reflexed when dry, erect-spreading when wet, acuminate, narrowly tapered, long decurrent, biplicate at base; margins plane above, narrowly recurved near base, entire to serrulate above; costae strong, percurrent, in cross section with rounded, thick-walled, homogenous cells, guide cells absent, stereid cells absent; cells smooth and thick-walled, upper and median cells rhombic, fusiform or elongate, at times porose; basal marginal cells quadrate to rectangular, cells near the insertions rectangular to fusiform. Autoicous. Perigonia terminal on short or long branches; perichaetia terminal on long branches. Setae short. Capsules immersed, ovoid to oblong-ovoid, abruptly rounded-indented to the setae; stomata absent; opercula conic; annuli compound; peristome diplolepideous, deeply inserted within the mouth; exostome teeth narrowly triangular to linear; endostome segments linear, cilia absent, basal membranes very low. Calyptrae conic.

Dendropogonella is a monospecific genus restricted to the Neotropics. It has a very distinctive habit: long, slender stems hanging in dense festoons from tree trunks and branches. This festooning habit along with its slender stems and reddish yellow color separates it from all other Central American members of Cryphaeaceae. Within the Cryphaeaceae only *Pilotrichopsis* and *Cyptodontopsis* have a somewhat similar pendent habit. These genera differ from *Dendropogonella* in having perichaetia at the ends of short, bud-like lateral branches rather than terminal at the ends of long branches. *Pilotrichopsis* also differs from *Dendropogonella* in having oval to elliptic median leaf cells, while *Cyptodontopsis* has a single peristome.

The placement of *Dendropogonella* in Cryphaeaceae is based on its oblong-ovoid, immersed capsules, reduced peristome, single costae, and quadrate to short-rectangular, basal marginal leaf cells. Within the Cryphaeaceae *Dendropogonella* is usually associated with those genera that have terminal perichaetia at the ends of long branches: *Schoenobryum*, *Dendrocryphaea*, and *Cyptodon*. The value of this feature as an indicator of family relationships is doubtful since the genera characterized as having "lateral perichaetia" actually have perichaetia at the ends of short branches. When its odd pendent habit is de-emphasized, *Dendropogonella* appears gametophytically closest to *Cryphaea*, which has some species with similar lanceolate, long-decurrent leaves, and elongate median leaf cells. *Dendropogonella* has smooth exostome teeth while *Cryphaea* (Gradstein *et al.* 2001) is usually considered to have papillose exostome teeth; however, smooth exostome teeth occasionally occur in *Cryphaea* (Rao 2001). *Dendropogonella* and *Cryphaea* also have capsules that are rounded-indented to the setae attachment, which results in a "pouch-like" (Buck 1998) capsule base. Manuel (1973b) revised *Dendropogonella.*

The name *Dendropogonella* combines the Greek *dendro* (tree) and *pogon* (beard) with the Latin diminutive *-ella* or "little tree beard," an obvious reference to the pendent, festooning habit of the genus.

Dendropogonella rufescens (Schimp.) E. Britton, Bryologist 9: 39. 1906. *Dendropogon rufescens* Schimp., Bot. Zeitung (Berlin) 1: 381. 1843. *Cryphaea rufescens* (Schimp.) Müll. Hal., Linnaea 18: 682. 1844 [1845]. *Pilotrichum rufescens* (Schimp.) Müll. Hal., Syn. Musc. Frond. 2: 176.

1851. Protologue. In sylvis mexicanis editioribus, ubi ad arborum ramos Alectoriae instar barbas longissimas efficit. A cll. *Karwinski*, *C. Ehrenberg* et a. lectum. Type (see Manuel 1973b). [Mexico] *Ehrenberg s.n.* (BM, lectotype).

Plants slender, pendent in reddish brown to dull red festoons, yellow green at tips of stems and branches. Stems flexuose, slender, to 30 cm long, irregularly pinnately branched; cross section with sclerodermis of 3–5 rows of very small, red brown, thick-walled cells, cortical cells enlarged, yellow, thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia foliose; rhizoids rarely seen, restricted to parts of stems that touch the substrate, red, short, smooth, not or rarely branched, from clusters of initials abaxial to the leaf insertions. Stem and branch leaves narrowly lanceolate, stem leaves 2–3 mm long, branch leaves 1–2 mm long, imbricate to reflexed when dry, erect-spreading when wet, acuminate, narrowly tapered, long-decurrent, biplicate at base; margins plane above, narrowly recurved near base, entire to serrulate above; costae strong, percurrent, in cross section with rounded, thick-walled homogenous cells, guide cells absent, stereid cells absent; cells smooth and thick-walled, upper and median cells rhombic, fusiform or elongate, at times porose, 20–45 µm long; basal marginal cells quadrate to rectangular, 9–14 µm; cells near the insertions rectangular to fusiform, 11–23 µm long. Autoicous. Perigonia terminal on short or long branches, outer leaves ovate, narrowly acuminate, 1.5–2.0 mm long, inner leaves oval; perichaetia terminal on long branches, outer leaves linear to 3.0 mm long, costae long excurrent into a spinose awn, inner leaves elliptic. Setae short, to 0.4 µm long, red, cells quadrate. Capsules immersed, ovoid to oblong-ovoid, 1.0–1.5 mm long, smooth, light brown, narrowed at the mouth, abruptly rounded-indented to the setae; exothecial cells small, red, in 2–3 rows below the mouth, irregularly quadrate to rectangular below; stomata absent; opercula conic, smooth, 0.5 mm long; annuli compound; peristome diplolepideous, deeply inserted within the mouth; exostome teeth narrowly triangular to linear, white to yellow, 0.25–0.28 mm long; endostome segments linear, smooth, shorter than the exostome, cilia absent, basal membranes very low. Spores spherical, lightly papillose, 14–21 µm. Calyptrae conic, smooth, basally split, 1.0 mm long.

Illustrations. Schimper (1843, Figs. 1–21); Brotherus (1905a, Figs. 551 L–N & 557); Brotherus (1925, Figs. 490 L–N & 493); Bartram (1949, Fig. 108 G–H); Crum and Steere (1957, Fig. 34); Manuel (1973b, Figs. 2–14); Sharp *et al.* (1994, Fig. 518); Gradstein *et al.* (2001, Fig. 104 G–M). Figure 19.

Habitat. Festooning or pendent from tree and shrub branches or twigs, occasionally on tree trunks, especially common in cloud forests; 2100–3600 m.

Distribution in Central America. GUATEMALA. El Progreso: *Steyermark 43673* (FH, MO, NY, US); Huehuetenango: *Steyermark 50553* (FH, MO, NY, TENN, US); Quetzaltenango: *Sharp 2253* (FH, TENN, US); San Marcos: *Sharp 5395a* (TENN) Sololá/Totonicapán: *Williams et al. 41755B* (MO); Tontonicapán: *Standley 62722* (FH). EL SALVADOR. Chalatenango: *Sipman 37628* (NY). HONDURAS. Lempira: *Allen 12239* (DUKE, MO); Santa Bárbara: *Allen 11665* (DUKE, MO). COSTA RICA. San José: *Standley 42649* (FH, NY, US); Limón: *Davidse et al. 29395B* (MO); Puntarenas: *Davidse et al. 23953* (MO). PANAMA. Chiriquí: *Allen 9065* (DUKE, MO).

World range: Mexico; Central America; Northern South America, Brazil.

Dendropogonella rufescens is a very slender, reddish yellow moss that grows pendent in dense festoons from branches and twigs. It has narrowly lanceolate, long-decurrent leaves with percurrent costae, quadrate to rectangular basal marginal cells, and fusiform to elongate median leaf cells. The species can be recognized in the field by its habit alone. Under the microscope the presence of fusiform to elongate median leaf cells separates it from all other Central American species of the *Cryphaeaceae* except *Cryphaea attenuata*. *Cryphaea attenuata*, however, grows in short mats with stiff, erect stems that are perpendicular to the substrate. It further differs from *D. rufescens* in having broader leaves with shorter costae (stem leaves 0.6–0.9, branch leaves 0.3–0.6 the leaf length). *Cryphaea jamesonii* has narrowly lanceolate leaves, which gives it an aspect somewhat like *D. rufescens*. That species differs from *D. rufescens* in having denticulate upper leaf margins and elliptic median leaf cells. The presence of strongly biplicate leaves in *D. rufescens* was used by Gradstein *et al.* (2001) to separate it from other members of the Cryphaeaceae, but this distinction is difficult to

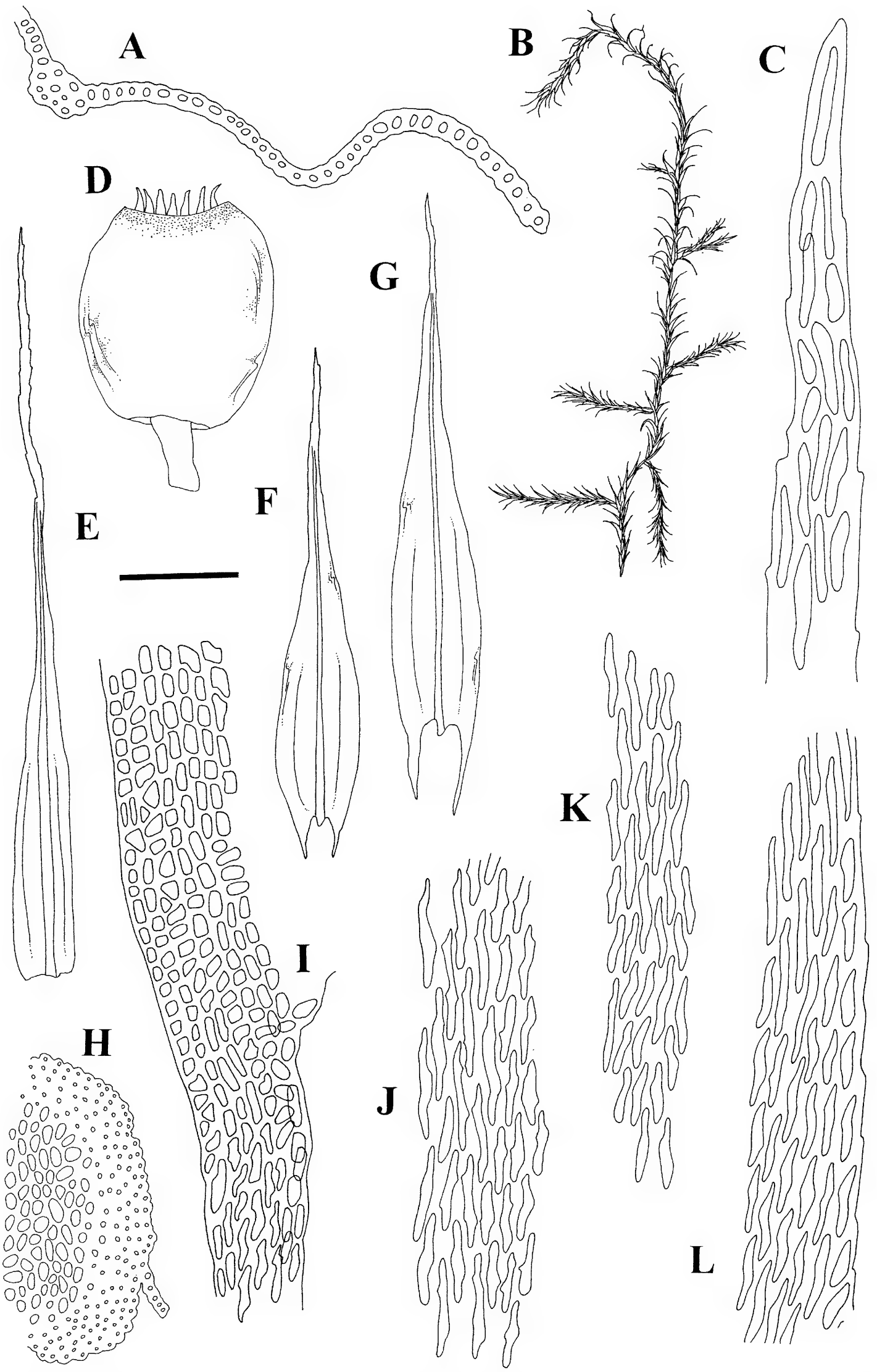
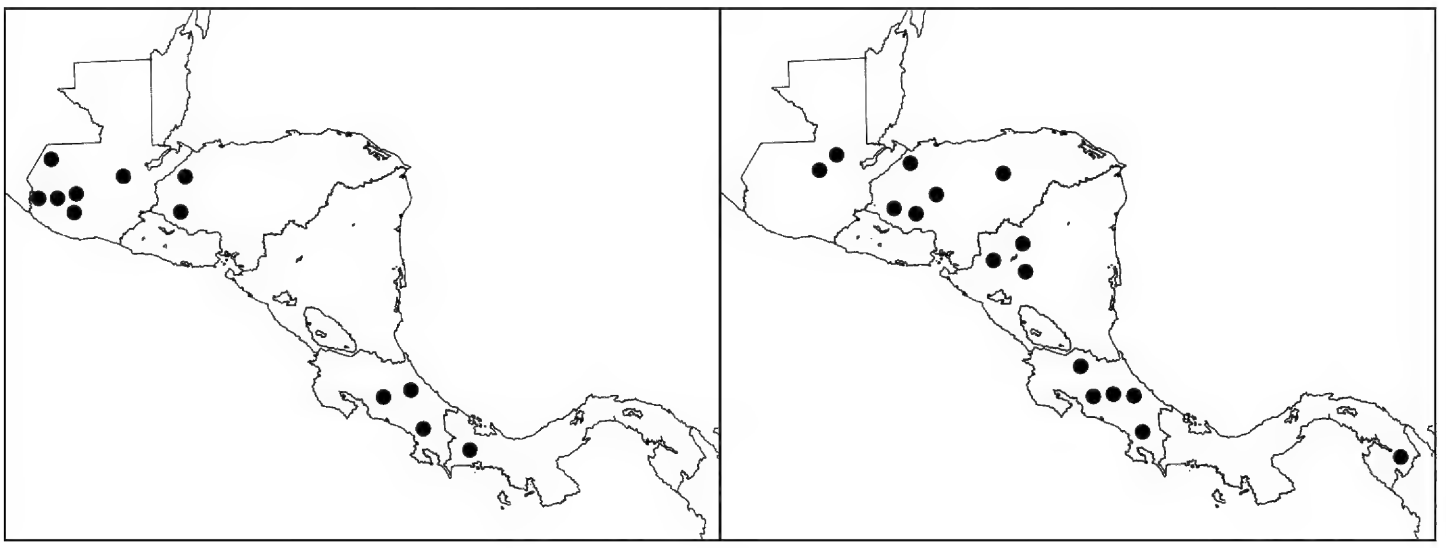


Figure 19. *Dendropogonella rufescens*. A. Leaf cross section. B. Habit. C. Leaf apex. D. Seta and capsule. E. Outer perichaetial leaf. F. Branch leaf. G. Stem leaf. H. Stem in cross section. I. Alar region. J. Lower median leaf cells. K. Upper median leaf cells. L. Leaf margin. Scale in mm: bar = 0.05 (A, C, I–L); bar = 0.06 (H); bar = 0.5 (E–G); bar = 0.6 (D); bar = 6.4 (B). D & E from *Sharp 2375d*; all other figure parts from *Allen 12177*.



Dendropogonella rufescens *Schoenobryum concavifolium*

apply because some *Cryphaea* species have variably plicate leaves. Rhizoids can be very difficult to find in herbarium material of *D. rufescens* because most collections contain only the pendent parts of the plant. Those collections that include the substrate, however, nearly always have rhizoids. The rhizoids are sometimes reported (Manuel 1973b) to be clustered in the leaf axils, but, as in other members of the Cryphaeaceae, the rhizoidal initials are abaxial and found just below the line of leaf insertion. Although *D. rufescens* is an autoicous species and many collections have terminal perigonia and perichaetia, some collections consist entirely of plants with either perigonia or perichaetia.

In Central America *Dendropogonella rufescens* is a cloud forest species restricted to high elevations. In the Caribbean, Britton (1906) reported it from St. Thomas, Virgin Islands. Manuel (1973b), however, saw no herbarium material of *D. rufescens* from St. Thomas nor did he find any cited specimens of it in the literature from St. Thomas. Not only is the climate of St. Thomas too dry for *D. rufescens*, but, as noted by Manuel (1973b), the island is too low to support that species.

3. *Schoenobryum* Dozy & Molk., Musci Frond. Ined. Archip. Ind. 6: 183. 1848.

Acrocryphaea Schimp. *in* B.S.G., Bryol. Eur. 5: 32. 1850 (fasc. 44–45), invalid name, lacks a description.
Cryphaea sect. *Acrocryphaea* Hook. & Wilson *ex* Mitt., J. Linn. Soc., Bot. 12: 410. 1869. *Acrocryphaea* (Mitt.) Besch., J. Bot. (Morot) 5: 342. 1891.

Plants medium-sized, in green or yellow green mats. Primary stems creeping, irregularly branched, leaves reduced; rhizoids red brown, from sparse clusters of initials at abaxial side of leaf insertions, not or rarely branched. Secondary stems erect, irregularly branched; stems in cross section with sclerodermis well developed, cortical cells enlarged, firm- or thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia subfoliose. Secondary stem and branch leaves ovate to ovate-lanceolate, imbricate or imbricate with erect-spreading apices when dry, spreading to wide-spreading when wet, acute to shortly acuminate, decurrent; margins plane or narrowly recurved, serrulate at the apex; costae strong, 0.4–0.8 the length of the leaves, occasionally spurred above; apical cells elliptic to linear, upper cells oval to elliptic, thick-walled, smooth or prorate, median cells oval to oblong; basal cells near the costa short-rectangular or variously elongate to linear, thick-walled, straight-walled or porose; alar cells quadrate, or oblate, thick-walled, smooth. Autoicous. Perigonia gemmate, borne laterally, leaves ovate, concave, acuminate, ecostate; perichaetia terminal, leaves erect, oblong to obovate, with long, serrate awns, margins recurved, costae long-excurrent, lower leaf cells linear, thin-walled. Setae short, cells quadrate. Capsules immersed, ovoid to ellipsoid, narrowed at the mouth, abruptly rounded-indented to the setae; exothecial cells small, red, in 2–3 rows below the mouth, irregularly quadrate to rectangular below; stomata superficial at junction of seta and capsule; opercula high-conic to short rostrate, smooth; annuli compound, revoluble; peristome diplolepideous; exostome teeth deeply inserted within the mouth, linear, whitish yellow or red, densely and thickly papillose with papillae often branched; endostome absent. Spores spherical, lightly papillose. Calyptrae conic-mitrate, prorate, basally split.

Schoenobryum is a pantropical genus of 16 species (Crosby *et al.* 2000). The genus is based on the presence of terminal perichaetia at the ends of stems or long branches, and single (exostomial) peristomes. *Cryphaea* and *Schoenobryum* have very similar gametophytes; indeed, the gametophytes of some *Cryphaea* species cannot be distinguished from those of *Schoenobryum*. *Cryphaea* differs from *Schoenobryum* in having lateral perichaetia at the ends of very short branches, and most (but not all) *Cryphaea* species have double peristomes. Buck (1998) noted that the exostome teeth in *Schoenobryum* have densely branched papillae, while those of *Cryphaea* have simple or little-branched papillae. *Schoenobryum* seems well founded, but the presence in *Cryphaea* of technically terminal perichaetia, albeit on short branches, and one species with a single peristome makes *Schoenobryum* considerably less distinct. In view of their very similar gametophytes it might be better to consider them subgenera rather than distinct genera.

The name *Schoenobryum* combines the Greek *schoinos* (rush-rope) and *bryon* (moss). It apparently refers to the dry, rope-like aspect of its dry stems.

1. Leaf margins plane; basal cells near costa short-rectangular . . . . . 2. *S. julaceum*
1. Leaf margins often recurved; basal cells near the costa elongate to linear 2

2. Leaf apices apiculate to gradually short-acuminate; apical leaf cells oval to oblong; perichaetial leaves gradually narrowed to the awn . . . . . 1. *S. concavifolium*
2. Leaf apices abruptly acuminate; apical leaf cells linear; perichaetial leaves abruptly rounded or contracted to the awn . . . . . 3. *S. rubricaule*

1. *Schoenobryum concavifolium* (Griff.) Gangulee, Mosses E. India 5: 1209. 1976. *Orthotrichum concavifolium* Griff., Calcutta J. Nat. Hist. 2: 484. 1842. *Cryphaea concavifolia* (Griff.) Mitt., J. Proc. Linn. Soc., Bot., Suppl. 2: 125. 1859. *Acrocryphaea concavifolia* (Griff.) Bosch & Sande Lac., Bryol. Jav. 2: 106. 1864, invalid combination, basionym not cited. *Schoenobryum concavifolium* (Griff.) Gangulee, Taxon. Indian Mosses 301. 1975, invalid combination, basionym not cited. *Schoenobryum concavifolium* (Griff.) Manuel, Bryologist 80: 523. 1977, superfluous combination. Protologue. [India] Inveni specimen unicum fructiferum mixtum cum *Neckera aurea* e Mumbree [*Griffith*].

Cryphaea gardneri Mitt., J. Linn. Soc., Bot., Suppl. 1: 125. 1859. *Acrocryphaea gardneri* (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1874–75: 178. 1876, invalid combination, genus invalid. *Schoenobryum gardneri* (Mitt.) Manuel, Bryologist 80: 523. 1977. Protologue. A beato *Gardner* in Brasilia lecta et sub *No. 75*. Type (see Manuel 1981). Minas Gerais, *Gardner 75* (BM, lectotype).

Acrocryphaea mexicana Schimp. *ex* Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 217. 1872, invalid name, lacks a description and illegitimate name, includes an earlier name in synonymy. Based on: Mexico (*Leiboldt*, *Ghiesbreght* in herb. Mus. Paris); Mirador (*Sartorius*) (NY); Cordova (*Sallé* in herb Mus. Paris) (NY).

Acrocryphaea julacea var. *costaricensis* Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32(1): 175. 1893 [1894], invalid name, genus invalid. *Schoenobryum julaceum* var. *costaricensis* (Renauld & Cardot) Manuel, Bryologist 80: 523. 1977. Protologue. [Costa Rica] Boruca (*Pitt.*[*ier*] *n*^{o} *5610, 5611, 5612*). Type (see Manuel 1981). *Pittier 5611* (H, lectotype; BM, G, S, isolectotypes); *Pittier 5610* (BR, PC, syntypes); *Pittier 5612* (BR, PC, syntypes).

Cryphaea coffeae Müll. Hal., Hedwigia 37: 240. 1898. *Acrocryphaea coffeae* (Müll. Hal.) Paris, Index Bryol. Suppl. 1:1. 1900, invalid name, genus invalid. *Schoenobryum coffeae* (Müll. Hal.) Manuel, Bryologist 80: 523. 1977. Protologue. Cuba, ad frutices *Coffeae Arabicae*: *Charles Wright* 1856. Type (see Manuel 1981). Sullivant, *Musci Cubenses 67* (NY, lectotype).

Plants medium-sized, in green or yellow green mats. Primary stems creeping, irregularly branched, leaves reduced; rhizoids red brown, from sparse clusters of initials abaxial to the leaf insertions, not or rarely branched. Secondary stems erect, 2–4.5 cm long, irregularly branched; cross section with sclerodermis of 3–5 rows of small, orange to red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, firm- or thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia subfoliose. Secondary stem and branch leaves ovate to ovate-lanceolate, 1.0–1.8 mm long, imbricate when dry, spreading to wide-spreading when wet, acute to shortly acuminate, decurrent; margins nar-

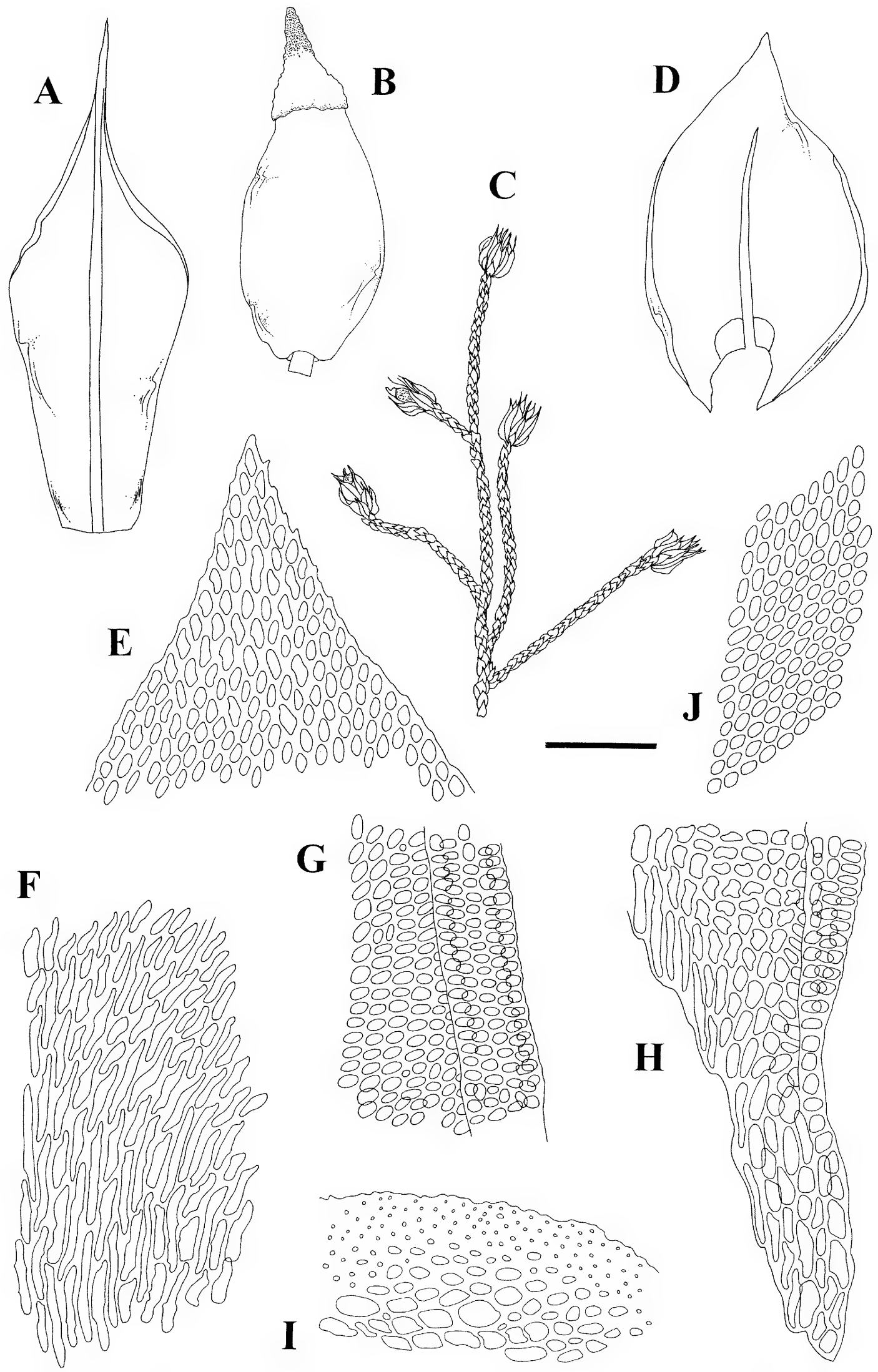


Figure 20. *Schoenobryum concavifolium*. A. Outer perichaetial leaf. B. Seta and capsule. C. Habit. D. Leaf. E. Leaf apex. F. Basal leaf cells near costa. G. Median leaf margin. H. Alar region. I. Stem in cross section. J. Basal cells. Scale in mm: bar = 0.06 (E–H, J); bar = 0.08 (I); bar = 0.5 (A, D); bar = 0.6 (B); bar = 5.1 (C). B & C from *Dauphin 2040*; A from *Allen 13698*; all other figure parts from *Allen 11829*.

rowly recurved in lower 1/2 or less, serrulate at the apex; costae strong, 0.4–0.6 the leaf length, occasionally spurred above; upper cells oval to elliptic, 10–20 µm long, very thick-walled, smooth or prorate, median cells oval, 12–16 µm long; basal cells near the costa elongate to linear, to 60 µm long, thick-walled, straight-walled or porose; alar cells quadrate, or oblate, thick-walled, smooth. Autoicous. Perigonia gemmate, borne laterally, leaves ovate, concave, acuminate, ecostate; perichaetia terminal, leaves erect, 2–3 mm long, oblong to obovate, gradually contracted to long, serrate awns, margins recurved, costae long-excurrent, lower leaf cells linear, thin-walled. Setae short, to 0.5 µm long, yellow to red, cells quadrate. Capsules immersed, ovoid to ellipsoid, 1.0–1.6 mm long, smooth, light brown, narrowed at the mouth, abruptly rounded-indented to the setae; exothecial cells small, red, in 2–3 rows below the mouth, irregularly quadrate to rectangular below; stomata superficial, at junction of seta and capsule; opercula high-conic to short rostrate, smooth, 0.5 mm long; annuli compound, revoluble; peristome diplolepideous; exostome teeth deeply inserted within the mouth, linear, red, densely and thickly papillose with papillae often branched, to 0.5 mm long; endostome absent. Spores spherical, lightly papillose, 20–30 µm. Calyptrae conic-mitrate, prorate, basally split, 0.5–0.7 mm long.

Illustrations. Bartram (1949, Fig. 107 A–C); Manuel (1981, Fig. 6 i–n); Sharp *et al.* (1994, Fig. 517); Churchill and Linares (1995, Fig. 54 a–g); Duarte Bello (1997, Pl. 175); Buck (1998, Pl. 65 1–9); Gradstein *et al.* (2001, Fig. 104 N–T). Figure 20.

Habitat. On trunks, branches, and twigs of trees and shrubs; 80–1872 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: *Johnson 243* (US); Baja Verapaz: *Sharp 2812a* (FH). HONDURAS. Comayagua: *Allen 13698* (MO, TEFH); Cortés: *Morton 7850* (US); Intibucá: *Standley 25518* (NY); Lempira: *Allen 11829* (MO); Olancho *Allen 12881* (MO). NICARAGUA. Estelí: *Stevens 16288* (MO); Jinotega: *Crosby 2744* (DUKE); Matagalpa: *Richards et al. 3721* (MO). COSTA RICA. Alajuela: *Crosby 10040* (MO); Cartago: *Schäfer-Verwimp & Holz SV/H-0376* (MO); Limón: *Gutiérrez s.n.* (FH); Puntarenas: *Dauphin 2040* (MO); San José: *King C-74-012* (MO). PANAMA. Darién: *Allen 8934* (MO).

World range: Southeastern U.S.A.; Mexico; Central America; Caribbean; Western, Northern, and Southern South America, Brazil; South and East Tropical Africa, Western Indian Ocean; China; Indian Subcontinent, Indo-China, Malesia; Australasia.

Schoenobryum concavifolium is the most commonly encountered species of *Schoenobryum* in Central America. Its ovate to ovate-lanceolate leaves are imbricate when dry with acute to broadly acuminate apices, short at times spurred costae, and mostly oval leaf cells. The apical leaf cells are often elliptic and the basal cells near the costae are linear in a fairly broad band. The leaf margins in *S. concavifolium* vary from strongly recurved in the lower half to recurved only at the base. The expression of *S. concavifolium* nomenclaturally centered on *S. coffeae* has weakly recurved leaf margins. Frequently collections of this expression have a mix of leaves with plane and recurved margins.

Schoenobryum julaceum was treated as a synonym of *S. concavifolium* by Dozy and Molkenboer (1865, as *Acrocryphaea concavifolia*), despite the fact that Mitten (1859) considered the two distinct. Although the two species are similar in aspect and leaf shape, *S. julaceum* has consistently plane leaf margins, juxtacostal leaf cells mostly short-rectangular with elongate cells restricted to the very leaf base, and whitish yellow exostome teeth. *Schoenobryum rubricaule* differs from *S. concavifolium* in having abruptly long apiculate leaves, longer, narrower apical leaf cells, and perichaetial leaves that are abruptly contracted to the awns.

In the absence of sporophytes *Schoenobryum concavifolium* can be confused with *Sphaerotheciella polycarpa*, *Sphaerotheciella pinnata*, and *Cryphaea patens* because they all have similar leaf shapes and areolation. In *Sphaerotheciella polycarpa*, however, the leaves have entire upper margins and are somewhat larger than those of *Schoenobryum concavifolium*. *Sphaerotheciella pinnata* and *Cryphaea patens* have sharply serrate to coarsely denticulate upper leaf margins, and their leaves are also somewhat larger than those of *Schoenobryum concavifolium*. *Cryphaea patens* also often has twisted leaf apices, and this feature does not occur in *Schoenobryum concavifolium*.

2. *Schoenobryum julaceum* Dozy & Molk., Musci Frond. Ined. Archip. Ind. 6: 184. 1848, new name for *Grimmia julacea* Hornsch. *in* Mart., 1840. *Grimmia julacea* Hornsch. *in* Mart., Fl. Bras. 1(2): 7. 1840, illegitimate homonym. Not *Grimmia julacea* (Hedw.) F. Weber & D. Mohr, 1803. *Acrocryphaea julacea* (Dozy & Molk.) Schimp. *in* B.S.G., Bryol. Eur. 5: 32. 1850 (fasc. 44–45), invalid combination, genus invalid. *Pilotrichum julaceum* (Dozy & Molk.) Müll. Hal., Syn. Musc. Frond. 2: 173. 1851. *Cryphaea julacea* (Dozy & Molk.) Mitt., J. Linn. Soc., Bot. 12: 415. 1869. *Schoenobryum julaceum* (Hornsch.) Yano, Bol. Inst. Bot. (São Paulo) 10: 127. 1996, invalid combination, basionym not cited and illegitimate homonym. Not *Schoenobryum julaceum* Dozy & Molk., 1848. Protologue. [Brazil] In Serra dos Orgaôs [sic], supér saxa rivorum, Januario mense, Junio mense in truncis arborum: *Beyrich*; in sylvis udis, in vetustis truncis fluctuantibus fluminis Amazonum: *M*[*artius*].

Plants medium-sized, in green or yellow green mats. Primary stems creeping, irregularly branched, leaves reduced; rhizoids red brown, from clusters of initials abaxial to the leaf insertions, not or rarely branched. Secondary stems erect, 2–4.5 cm long, irregularly branched; cross section with sclerodermis of 3–5 rows of small, orange to red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, firm- or thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia subfoliose. Secondary stem and branch leaves ovate to broadly ovate-lanceolate, 1.0–1.7 mm long, imbricate when dry, spreading to wide-spreading when wet, acute to shortly acuminate, decurrent; margins plane, serrulate at the apex; costae strong, 0.4–0.6 the leaf length; upper cells oval to elliptic, 12–16 µm long, very thick-walled, smooth or prorate, median cells oval, 12–18 µm long; basal cells near the costae short-rectangular, thick-walled, to 35 µm long, with straight or occasionally porose cell walls; alar cells quadrate, or oblate, thick-walled, smooth. Autoicous. Perigonia gemmate, borne laterally, leaves ovate, concave, acuminate, ecostate; perichaetia terminal, leaves erect, oblong to obovate, 2–3 mm long, gradually contracted to long, serrate awns, margins recurved, costae long-excurrent, lower leaf cells linear, thin-walled. Setae short, to 0.5 µm long, yellow to red, cells quadrate. Capsules immersed, ovoid to ellipsoid, 1.3–1.8 mm long, smooth, light brown, narrowed at the mouth, abruptly rounded-indented to the setae; exothecial cells small, red, in 2–3 rows below the mouth, irregularly quadrate to rectangular below; stomata superficial, at junction of seta and capsule; opercula high-conic to short rostrate, smooth, 0.5 mm long; annuli compound, revoluble; peristome diplolepideous; exostome teeth deeply inserted within the mouth, linear, whitish yellow, densely and thickly papillose with papillae often branched, to 0.5 mm long; endostome absent. Spores spherical, lightly papillose, 20–30 µm. Calyptrae conic-mitrate, prorate, basally split, 0.5–0.7 mm long.

Illustration. Figure 21.

Habitat. On bark at base of shrubs, tree trunks, and (*Erythrina*) branches, on fence posts and logs; 200–1080 m.

Distribution in Central America. HONDURAS. Comayagua: *Allen 13402* (MO, TEFH); Copán: *Allen 17667* (MO); Yoro: *Allen 13535* (MO). NICARAGUA. Boaco: *Stevens 5913A* (MO).

World range: Mexico; Central America; Brazil.

Schoenobryum julaceum is distinguished from the other Central American species of *Schoenobryum* by its consistently plane leaf margins. This feature must be carefully evaluated, however, because the perichaetial leaves and subperichaetial leaves of *S. julaceum* have recurved margins. The leaves of *S. concavifolium* are somewhat variable in margin stance, and, although occasional collections of the species have leaves with plane margins, other leaves in the same collections can be found with recurved margins. *Schoenobryum concavifolium* also differs from *S. julaceum* in having reddish exostome teeth and elongate, porose juxtacostal cells that radiate in a broad band from the leaf base. *Schoenobryum rubricaule* differs from *S. julaceum* in its abruptly long-acuminate leaf apices and outer perichaetial leaves that abruptly contract to the awns.

When sporophytes are absent, *Schoenobryum julaceum* is very difficult to distinguish from *Cryphaea filiformis* and *C. orizabae* because they all have similar shaped leaves with plane margins. *Schoenobryum julaceum* differs somewhat from the other two species in features of its leaf apices. In *S. julaceum* the apices are narrowly acute to broadly acuminate, and consistently serrulate. *Cryphaea filiformis* and *C. orizabae* have narrowly acuminate leaf apices that vary from serrulate to entire.

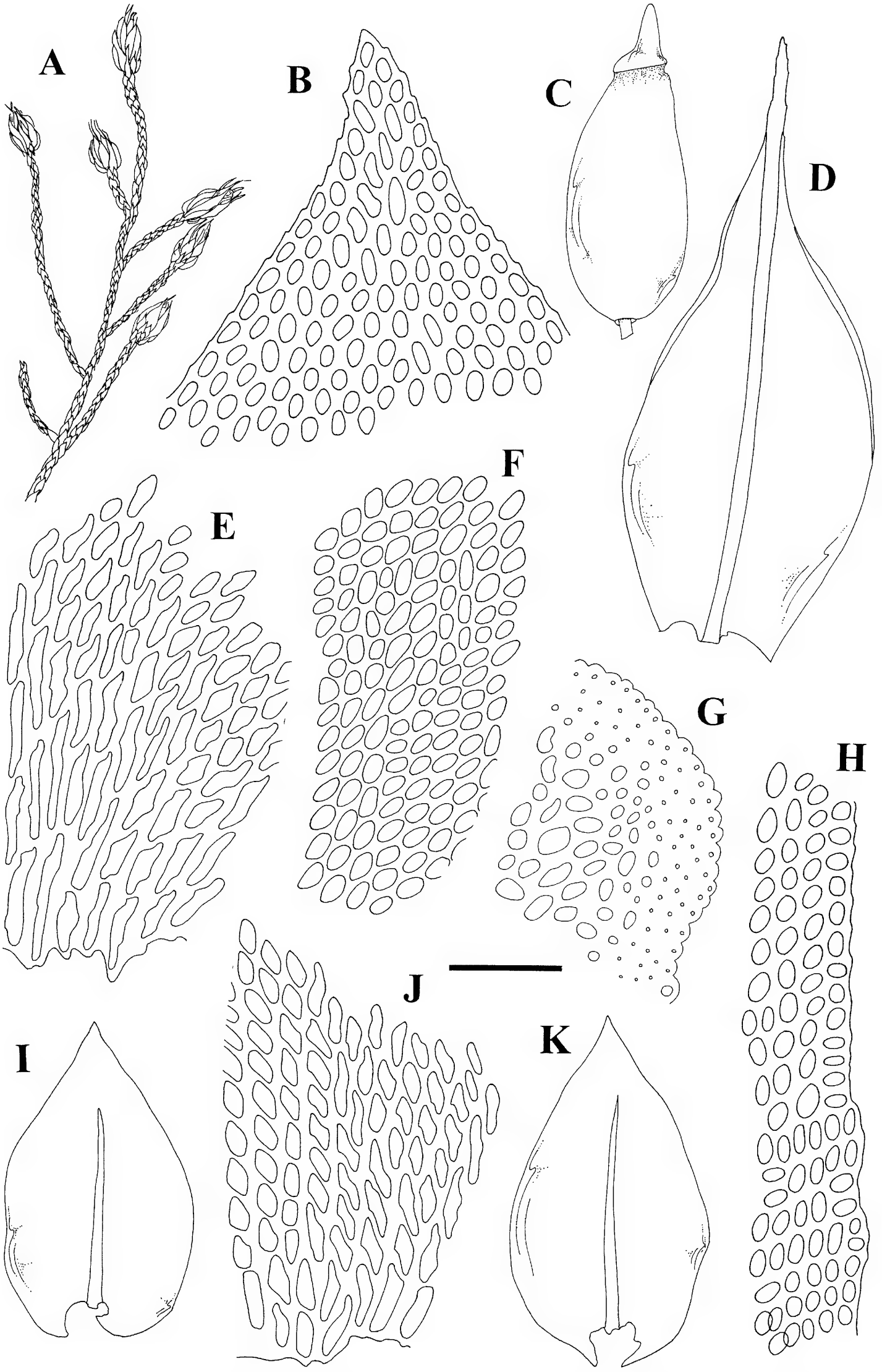
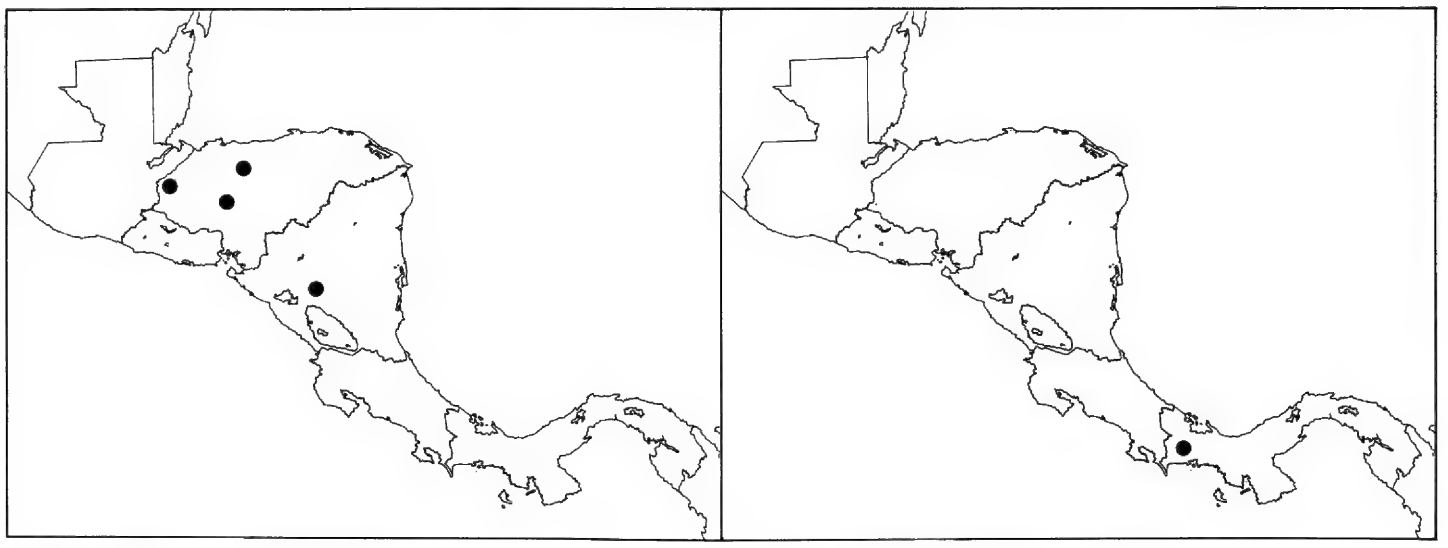


Figure 21. *Schoenobryum julaceum*. A. Habit. B. Leaf apex. C. Seta and capsule. D. Perichaetial leaf. E. Basal cells near costa. F. Median leaf cells. G. Stem in cross section. H. Leaf margin. I & K. Leaves. J. Basal cells near margin. Scale in mm: bar = 0.05 (B, E, F, H, J); bar = 0.06 (G); bar = 0.5 (D, I, K); bar = 0.6 (C); bar = 5.1 (A). A, C, D, G from *Allen 13402*; all other figure parts from *Allen 13677*.



Schoenobryum julaceum *Schoenobryum rubricaule*

These distinctions are not always clear, and without the benefit of comparative material the gametophytic separation of the three species is problematical. The leaf apices of *C. filiformis* are often twisted, and this feature can be used to distinguish it from *S. julaceum*, which has plane leaf apices.

Schoenobryum julaceum has often been confused with *S. concavifolium*, partly because Bosch and Sande Lacoste (1865) treated them as synonyms. The original confusion surrounding the two species seems to have come from the erroneous use by Dozy and Molkenboer (1848) of the Brazilian name *Grimmia julacea* for the East Asian *S. concavifolium*. The situation is further complicated because the East Asian *S. concavifolium* is also present in the Neotropics (previously known as *S. gardneri*).

3. *Schoenobryum rubricaule* (Mitt.) Manuel, Bryologist 80: 523. 1977. *Cryphaea rubricaulis* Mitt., J. Linn. Soc., Bot. 12: 415. 1869. *Acrocryphaea rubricaulis* (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1874–75: 179. 1876. Protologue. [Ecuador] Andes Quitenses, prope Baños in ramulis, Lucmas, in valle Alausi (6000 ped.), *Spruce, n. 1285*.

Cryphaea mittenii A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1874–75: 180. 1876. New name for *Cryphaea apiculata* Mitt., J. Linn. Soc., Bot. 12: 411. 1869, not *Cryphaea apiculata* Schimp. *in* B.S.G., Bryol. Eur. 5: 35. 1850 (fasc. 44–45). *Schoenobryum mittenii* (A. Jaeger) Manuel, J. Hattori Bot. Lab. 49: 134. 1981. Protologue. [Panama] America centralis, Gorgona, *Seemann* (NY).

Plants medium-sized, in green or yellow green mats. Primary stems creeping, irregularly branched, leaves reduced; rhizoids red brown, from sparse clusters of initials abaxial to the leaf insertions, not or rarely branched. Secondary stems erect, to 4 cm long, irregularly branched; cross section with sclerodermis of 3–5 rows of small, orange to red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, firm- or thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia subfoliose. Secondary stem leaves ovate, branch leaves ovate to ovate-lanceolate, 1.2–1.7 mm long, imbricate with erect-spreading apices when dry, spreading to wide-spreading when wet, abruptly long- or short-acuminate, decurrent; margins narrowly recurved in upper 1/4, serrulate above; costae strong, 0.4–0.8 the length of the leaves; apical cells linear, upper cells elliptic to oblong, 11–20 µm long, very thick-walled, smooth or prorate, median cells oblong, 11–18 µm long; basal cells near the costae elongate to linear, to 60 µm long, thick-walled, straight-walled or porose, radiating outward from the costae in a broad band; alar cells quadrate, or oblate, thick-walled, smooth. Autoicous. Perigonia gemmate, borne laterally, leaves ovate, concave, acuminate, ecostate; perichaetia terminal, leaves erect, oblong to obovate, 2.5–3.5 mm long, abruptly rounded or truncate to long, serrate awns, margins recurved, costae long-excurrent, lower leaf cells linear, thin-walled. Setae short, to 0.5 µm long, cells quadrate. Capsules immersed, ovoid to ellipsoid, 1.0–1.8 mm long, smooth, light brown, narrowed at the mouth, abruptly rounded-indented to the setae; exothecial cells small, red, in 2–3 rows below the mouth, irregularly quadrate to rectangular below; stomata superficial at junction of seta and capsule; operculum not seen; annulus not seen; peristome diplolepideous, intact peristome

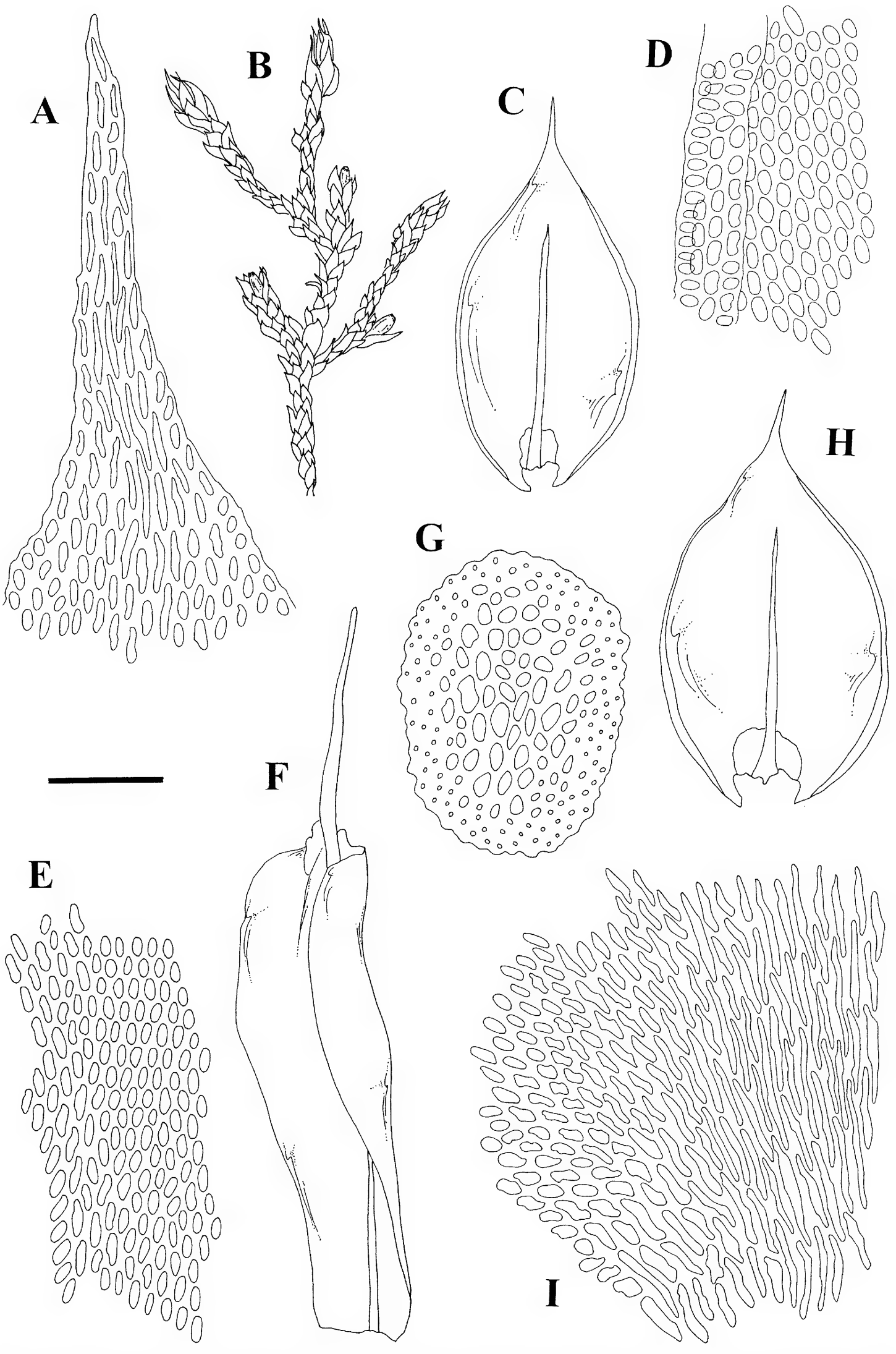


Figure 22. *Schoenobryum rubricaule*. A. Leaf apex. B. Habit. C & H. Leaves. D. Median leaf margin. E. Median leaf cells. F. Perichaetial leaf. G. Stem in cross section. I. Basal leaf cells near costa. Scale in mm: bar = 0.05 (D); bar = 0.08 (A, E, G, I); bar = 0.5 (C, H, F); bar = 4.3 (B). All figure parts from *Cornman 3168*.

not seen; exostome teeth deeply inserted within the mouth, linear, whitish, densely and thickly papillose; endostome absent. Spores spherical, lightly papillose, 20–25 µm. Calyptra not seen.

Illustrations. Manuel (1981, Fig. 6 i–n); Churchill and Linares (1995, Fig. 54). Figure 22.
Habitat. On branches of trees and shrubs: 1300–1800 m.
Distribution in Central America. PANAMA. Chiriquí: *Cornman 3168* (FH, MO, PMA, US).
World range: Central America; Western South America, Brazil.

Schoenobryum rubricaule is uncommon in Central America and is presently known only from Panama. The species has leaves with strongly recurved margins that are abruptly long-acuminate, and elongate to linear apical leaf cells. No other Central American species of *Schoenobryum* has this combination of features. Furthermore, in *S. concavifolium* and *S. julaceum* the perichaetial leaves are gradually narrowed to the awn, while the upper leaf margins of *S. rubricaule* are abruptly narrowed or truncate to the awn. The basal juxtacostal leaf cells in *S. rubricaule* are strongly differentiated in a broad band of elongate to linear leaf cells. Although *S. concavifolium* has similar basal juxtacostal leaf cells, they are not nearly as well developed as those of *S. rubricaule*.

When sporophytes are absent, plants of *Schoenobryum rubricaule* closely resemble *Sphaerotheciella gracillima* and *Cryphaea apiculata*. All three species have similarly shaped, abruptly long-acuminate leaves with strongly recurved margins and well-developed, elongate basal juxtacostal cells. The leaves of *Sphaerotheciella gracillima* are longer acuminate than those of *Schoenobryum rubricaule* and its upper leaf cells near the costa are elongate. The upper leaf cells near the costa in *Schoenobryum rubricaule* are elliptic to oblong. *Schoenobryum rubricaule* and *C. apiculata* are essentially indistinguishable when sporophytes and well-developed perichaetia are absent.

4. *Sphaerotheciella* M. Fleisch., Hedwigia 55: 282. 1914.

Plants medium-sized, in mats. Primary stems creeping; rhizoids from clusters of initials abaxial to the leaf insertions, red, smooth, unbranched or rarely irregularly branched. Secondary stems horizontal or erect, irregularly branched; cross section with sclerodermis, enlarged cortical cells, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous or subfoliose and with scale leaves. Secondary stem and branch leaves ovate, elliptic, or ovate-lanceolate, acute or acuminate, decurrent; margins revolute below, smooth, crenulate, serrate or denticulate above; costae single, strong, ending well below the apices; cells smooth and thick-walled, apical cells elliptic, fusiform or linear, upper cells oval to elliptic, median cells round, elliptic, or elongate; basal cells near the costae elongate to linear; alar cells short-rectangular, subquadrate, or oblate. Autoicous. Perichaetia and perigonia lateral. Perigonia gemmate, inner leaves ovate, ecostate; perichaetial leaves oblong to oblong-lanceolate, inner ones abruptly narrowed to a long, smooth or lightly roughened awn, equal to or somewhat shorter than the leaf lamina. Setae short, cells quadrate. Capsules immersed, ellipsoid, abruptly rounded-indented to the setae; exothecial cells small, red, in 2–3 rows below the mouth; stomata superficial, at junction of capsule and seta; opercula conic-rostrate; annuli compound, revoluble; peristome diplolepideous, inserted within the mouth; exostome teeth linear; endostome segments shorter than the exostome, cilia rudimentary or absent, basal membranes very low. Spores massive, spherical or irregularly oblong. Spores endosporically germinated within the capsule. Calyptrae mitrate-lacerate, smooth or prorate above.

Sphaerotheciella is a genus of six species found in the Neotropics (four species) and Asia (two species). The genus was established by Fleischer (1914) for a *Cryphaea* species with globular capsules and abnormally large, many-celled spores (*i.e.*, endosporically germinated protonemata). Although the Asian species of *Sphaerotheciella* appear to have globose to subglobose capsules, the Neotropical species have ellipsoid or occasionally (in *S. gracillima*) short-cylindrical capsules. The genus therefore is distinguished from *Cryphaea* only in having endosporically germinated protonemata.

A closer examination of the endosporically germinated protonemata in the genus, however, indicates that it actually represents two characters. As the capsules mature, the spores swell to a massive size (to 60 µm) but remain single-celled. In some mosses (*e.g.*, *Pilotrichella flexilis* (Hedw.) Ångstr.), development goes no further and the spores are released in this form. In *Sphaerotheciella* and other

mosses (*e.g.*, Dicnemonaceae, *Mesotus* Mitt., *Drummondia* Hook., *Muelleria* Dusén, *Leucodon* Schwägr., and *Bryowijkia* Nog.), the massive spores undergo endosporic germination within the capsule. In these mosses, with the exception of *Leucodon*, the presence of endosporically germinated protonemata is considered a feature of generic importance.

Much of the Central American material of *Sphaerotheciella* either lacks sporophytes or has capsules that no longer contain endosporically germinated protonemata. Indeed, unless mature capsules with intact opercula are present, it is very difficult to find any endosporically germinated protonemata. The same curiously empty capsules have been encountered in the Dicnemonaceae and *Drummondia*, and I am inclined to think insects are responsible for removing the massive diaspores.

Rao (2001) synonymized *Cryphaea macrospora* Herzog with *Cryphaea apiculata*. The former species, however, has massive spores that are endosporically germinated and so belongs in *Sphaerotheciella*. [*Sphaerotheciella macrospora* (Herzog) B. H. Allen, *comb. nov.*, basionym: *Cryphaea macrospora* Herzog, Biblioth. Bot. 87: 108. 1916. Protologue. Bolivia. Auf Baumästen im oberen Coranital, ca. 2600 m, [*Herzog*] *3370*.]

The name *Sphaerotheciella* combines the Greek *sphaero* (globose or spherical) with *theca* (container), and the Latin diminutive suffix *-ella*. It refers to the globose capsules of the type species (*S. sphaerocarpa* (Hook.) M. Fleisch.).

1. Upper leaf margins serrate to denticulate . . . . . 3. *S. pinnata*
1. Upper leaf margins entire, crenulate 2

2. Leaves ovate-lanceolate, abruptly long and narrowly acuminate; apical leaf cells elongate to linear . . . . . 1. *S. gracillima*
2. Leaves broadly ovate to elliptic, acute to short and broadly acuminate; apical leaf cells oval to elliptic . . . . . 2. *S. pachycarpa*

1. *Sphaerotheciella gracillima* (Herzog) B. H. Allen, *comb. nov*. Basionym: *Cryphaea gracillima* Herzog, Biblioth. Bot. 87: 107. 1916. Protologue. [Bolivia] Im Bergwald des Rio Tocorani, ca. 2600 m, [*Herzog*] *No. 4115*; im Nebelwald über Comarapa, ca. 2600 m, [*Herzog*] *No. 4257/a*. Type (see Rao 2001). Im Bergwald des Río Tocorani, ca. 2600 m, VII.1911, *Th. Herzog 4115* (JE, lectotype; S, isolectotype).

Plants medium-sized, in green or yellow green mats. Primary stems creeping, irregularly branched; rhizoids from clusters of initials abaxial to the leaf insertions, red, smooth, unbranched or rarely irregularly branched. Secondary stems horizontal or erect and loosely spreading, to 6 cm long, irregularly branched; cross section with sclerodermis of 3–6 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, very thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous or subfoliose and with scale leaves. Secondary stem and branch leaves ovate-lanceolate, stem leaves 1.5–2.0 mm long, branch leaves 1.0–1.5 mm long, erect to loosely imbricate, at times wrinkled when dry, erect-spreading when wet, narrowly acuminate, decurrent; margins revolute in lower 3/4 or less, smooth to crenulate above; costa strong, 0.4–0.6 the leaf length; cells smooth and thick-walled, cells in apex fusiform to linear, upper cells narrowly elliptic, 18–30 µm long, median cells elliptic to elongate; basal cells near costa and extending along costa to the apex elongate to linear, to 40 µm long; alar cells short-rectangular, subquadrate, or oblate, 8–16 µm. Autoicous. Perichaetia and perigonia lateral. Perigonia 0.5–0.7 mm long, inner leaves ovate, ecostate; perichaetial leaves oblong, inner ones abruptly narrowed to a long, smooth or lightly roughened awn equal to or somewhat shorter than the leaf lamina, costae discontinuous, stoutly filling the apex, absent at base. Setae short, 0.1–0.2 µm long, cells quadrate. Capsules immersed, ellipsoid, 1.3–1.7 mm long, smooth, light brown, narrowed at the mouth, abruptly rounded-indented to the setae; exothecial cells small, red, in 2–3 rows below the mouth, irregularly short-rectangular below; stomata superficial, at junction of capsule and seta; opercula conic-rostrate, smooth, to 0.5 mm long; annuli compound, revoluble; peristome diplolepideous, inserted within the mouth; exostome teeth linear, whitish yellow, dorsal (outer) surface densely papillose, ventral (inner) surface smooth to lightly papillose, to 0.5 mm long; endostome segments linear, lightly papillose, half the length of the exostome, cilia rudimentary, basal membranes very low. Spores massive, spherical or irregularly

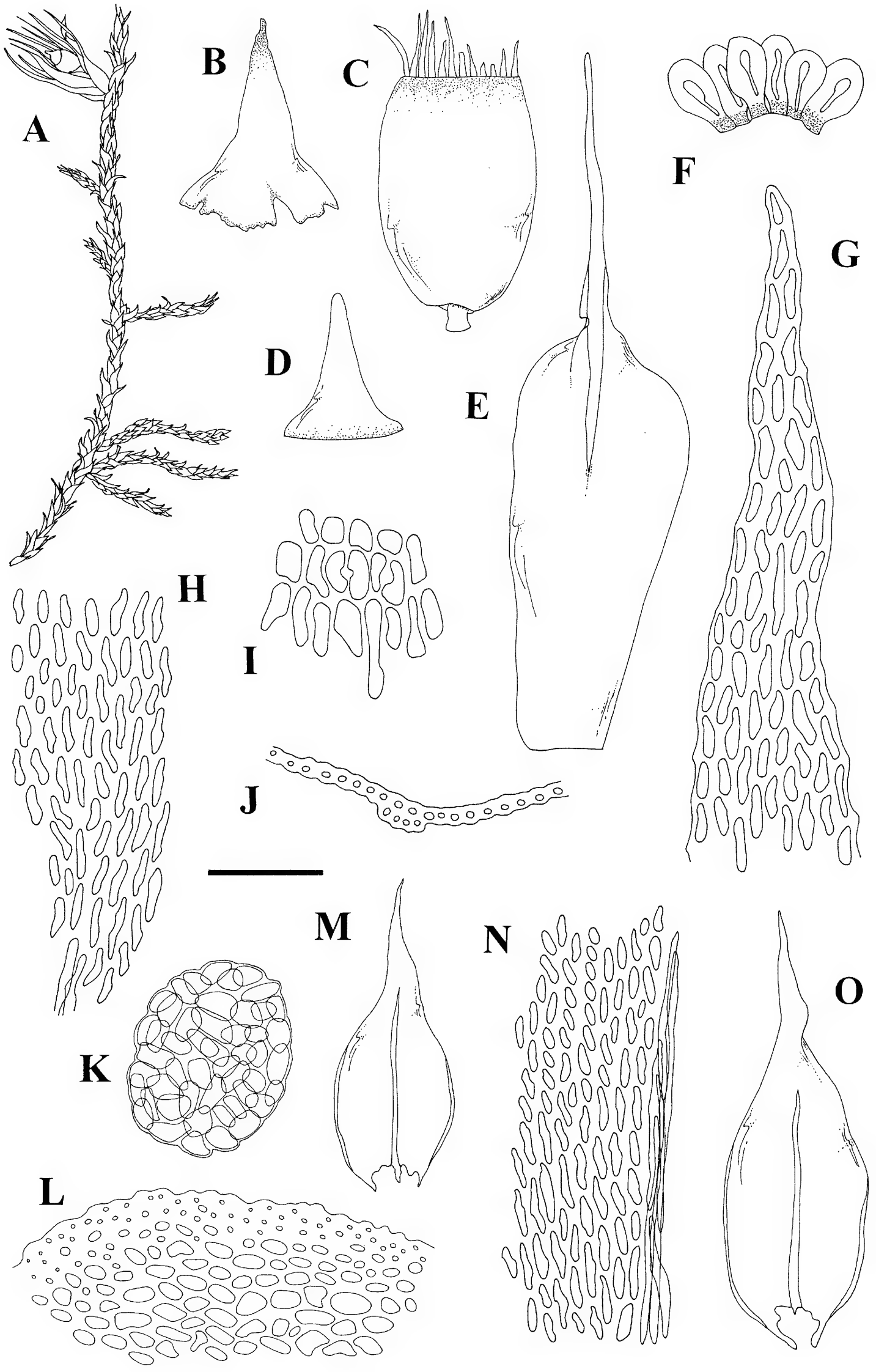
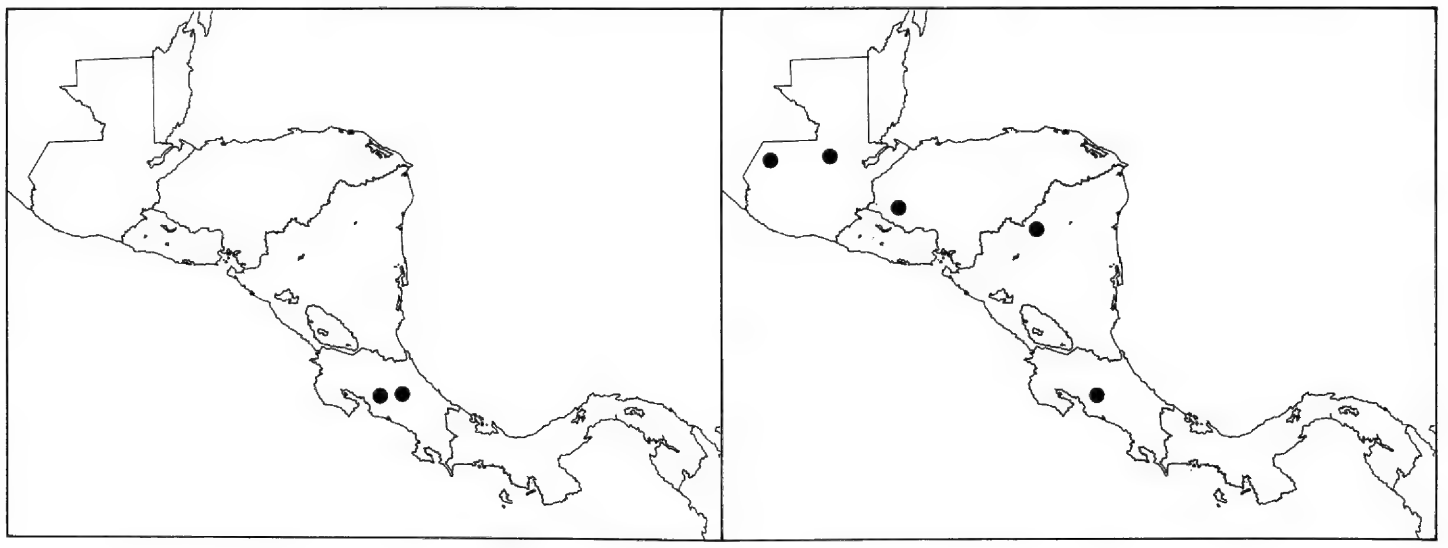


Figure 23. *Sphaerotheciella gracillima*. A. Habit. B. Calyptra. C. Seta and capsule. D. Operculum. E. Perichaetial leaf. F. Annulus. G. Leaf apex. H. Basal leaf cells. I. Stomata. J. Leaf in cross section. K. Endosporic protonemata. L. Stem in cross section. M & O. Leaves. N. Median cells near costa. Scale in mm: bar = 0.05 (G–J, N); bar = 0.06 (K, L); bar = 0.07 (F); bar = 0.36 (B, D); bar = 0.5 (M, O); bar = 0.6 (C, E); bar = 3.2 (A). All figure parts from *Hermann 29206*.



Sphaerotheciella gracillima *Sphaerotheciella pachycarpa*

oblong, smooth lightly papillose, to 60 µm. Spores endosporically germinated within the capsule, to 100 µm long. Calyptrae mitrate-lacerate, prorate above, 0.4–0.6 mm long.

Illustrations. Herzog (1916, Fig. 39); Rao (2001, Fig. 23). Figure 23.

Habitat. On trunks and branches of shrubs and trees; 2450–3300 m.

Distribution in Central America. COSTA RICA. Cartago: *Hermann 29206* (MO); San José: *Crosby & Crosby 6096* (MO).

World range: Central America; Western South America.

Sphaerotheciella gracillima has narrow, ovate-lanceolate leaves with entire to slightly crenulate leaf margins. The leaves are abruptly long-acuminate and as a result the costae are relatively short (to 0.6 the leaf length). As with other *Sphaerotheciella* species the basal leaf cells near the costa of *S. gracillima* are elongate. However, in *S. gracillima* these cells usually continue along the costa for as much as three-quarters the leaf length and sometimes they extend into the leaf acumina. Rao (2001) maintained *S. gracillima*, without comment, in *Cryphaea* even though Herzog (1916) clearly figured and described its multicellular, endosporic protonemata.

The leaves of *S. pachycarpa* and *S. gracillima* are similar in having entire to crenulate margins, but *S. pachycarpa* has ovate to elliptic leaves and short upper leaf cells. *Sphaerotheciella pinnata* is similar to *S. gracillima* in having ovate-lanceolate leaves, and often its apical leaf cells are fusiform. The leaves of *S. pinnata*, however, are broadly ovate-lanceolate, with serrate to dentate margins and elongate to linear basal cells near the costa only in the lower sixth of the leaf.

Sphaerotheciella gracillima is likely to be confused with *Cryphaea attenuata* or *C. apiculata* since all three species have narrowly acuminate leaves. In *C. apiculata*, however, the leaves are broadly ovate below the acuminate apex and its upper leaf cells are oval to elliptic. The leaves of *C. attenuata* and *S. gracillima* have long median leaf cells, and in shape they are more similar to each other than they are to the leaves of *C. apiculata*. *Cryphaea attenuata* differs from *S. gracillima* in having dimorphic stem and branch leaves. Furthermore, the stem leaves of *C. attenuata* are lanceolate rather than ovate-lanceolate, and all of the median leaf cells are linear. Most Central American collections of *S. gracillima* were originally named *C. attenuata*.

2. *Sphaerotheciella pachycarpa* (Schimp. *ex* Besch.) Manuel, J. Hattori Bot. Lab. 49: 136. 1981. *Cryphaea pachycarpa* Schimp. *ex* Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 215. 1872. Protologue. [Mexico] Mejico (*Deppe*); Chinantla (*Liebmann* in herb. Montagne); Orizaba (*Fr. Müller*). Type (see Manuel 1981). Mexico. Orizaba, *F. Müller s.n., p.p.* (BM, lectotype).

Plants medium-sized, in green or yellow green mats. Primary stems creeping, irregularly branched; rhizoids from clusters of initials abaxial to the leaf insertions, red, smooth, unbranched or

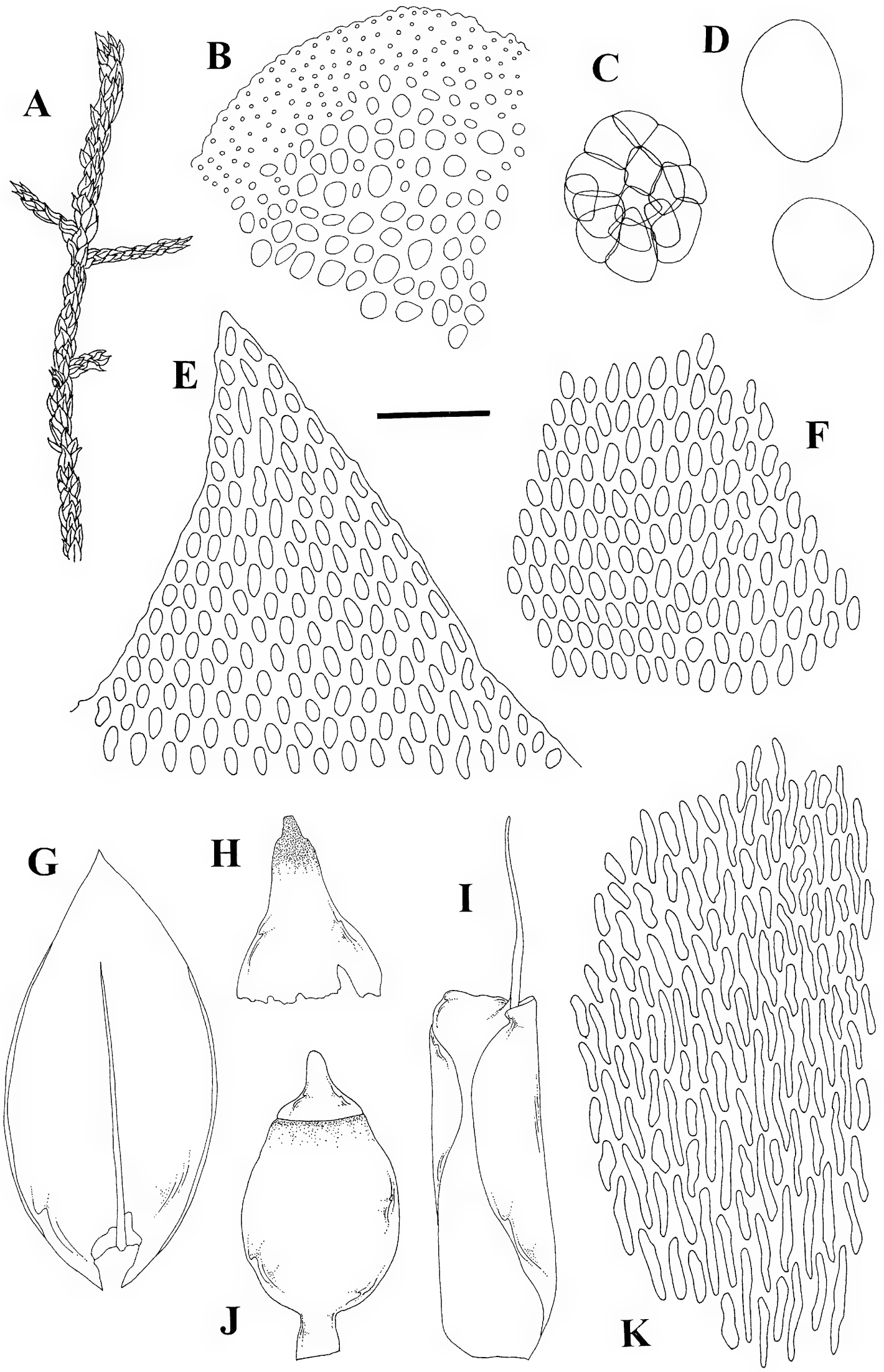


Figure 24. *Sphaerotheciella pachycarpa*. A. Habit. B. Stem in cross section. C. Endosporic protonemata. D. Spores. E. Leaf apex. F. Upper leaf cells. G. Leaf. H. Calyptra. I. Perichaetial leaf. J. Seta and capsule. K. Basal leaf cells near costa. Scale in mm: bar = 0.05 (C–F, K); bar = 0.06 (B); bar = 0.36 (H); bar = 0.6 (G, I) bar = 0.71 (J); bar = 5.4 (A). C from *Allen 11288B*; H–J from *Sharp 2909*; all other figure parts from *Crosby 9831*.

rarely irregularly branched. Secondary stems horizontal or erect and loosely spreading, to 5 cm long, irregularly branched; cross section with sclerodermis of 3–6 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, very thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous or subfoliose and with scale leaves. Secondary stem and branch leaves ovate to elliptic, 1.5–2 mm long, imbricate when dry, spreading when wet, acute to somewhat acuminate, decurrent; margins revolute in lower 3/4 or less, entire or crenulate above; costae strong, 0.6–0.8 the length of the leaves; cells smooth and thick-walled, upper cells oval to elliptic, 15–24 µm long, median cells round to elliptic, 10–20 µm long; basal cells near costa in lower 1/6 of leaf elongate to linear, to 50 µm long; alar cells short-rectangular, subquadrate, or oblate, 6–16 µm. Autoicous. Perichaetia and perigonia lateral. Perigonial leaves ovate; perichaetial leaves oblong to oblong-lanceolate, inner ones abruptly narrowed to a long, smooth awn, generally shorter than the leaf lamina, costae stoutly filling the apex, weakly developed or absent at base. Setae short, 0.1–0.2 µm long, cells quadrate. Capsules immersed, ellipsoid, 1.0–1.5 mm long, smooth, light brown, narrowed at the mouth, abruptly rounded-indented to the setae; exothecial cells small, red, in 2–3 rows below the mouth, irregularly short-rectangular below; stomata not seen; opercula conic-rostrate, smooth, to 0.5 mm long; annuli compound; peristome diplolepideous, inserted within the mouth; exostome teeth narrowly triangular to linear, whitish yellow, dorsal (outer) surface smooth below, papillose above, to 0.40 mm long; endostome segments linear, papillose, shorter than the exostome, cilia absent, basal membranes very low. Spores massive, spherical or irregularly oblong, lightly papillose, 44–65 µm. Spores endosporically germinated within the capsule, to 75 µm long. Calyptrae mitrate, smooth, 0.4–0.6 mm long.

Illustrations. Manuel (1981, Fig. 7); Sharp *et al.* (1994, Fig. 516 a–c). Figure 24.

Habitat. On tree trunks and twigs; 1400–2350 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: *Türckheim 7126* (H); Huehuetenango: *Sharp 4916B* (FH, TENN). HONDURAS. Lempira: *Allen 11279A* (MO). NICARAGUA. Jinotega: *Crosby 2733* (DUKE). COSTA RICA. San José: *Crosby 9831* (MO).

World range: Mexico; Central America; Northern South America.

Sphaerotheciella pachycarpa is a medium-sized species with ovate leaves that are imbricate when dry. Its leaves are acute to broadly acuminate with consistently recurved, entire or crenulate margins. *Sphaerotheciella pachycarpa* is the only Central American species in the Cryphaeaceae with this combination of features. The leaf illustrations in Sharp *et al.* (1994, Fig. 516 b & c) show serrulate upper leaf margins in *S. pachycarpa*, and the description indicates they can be entire or serrulate. Manuel (1981) described the leaf margins in *S. pachycarpa* as entire throughout, but in most Central American collections of *S. pachycarpa* they are lightly crenulate. *Sphaerotheciella pinnata* differs from *S. pachycarpa* in having clearly serrate to dentate upper leaf margins. The leaves of *S. pachycarpa* and *S. gracillima* have similar margins, but in *S. gracillima* the narrow, ovate-lanceolate leaves are abruptly long-acuminate, and the upper leaf cells are elongate to linear.

Central American *Cryphaea filiformis*, *C. orizabae*, and *C. apiculata* have entire to lightly serrulate leaf margins, which can cause confusion with *Sphaerotheciella pachycarpa*. The first two species differ from *S. pachycarpa* in having plane leaf margins. *Cryphaea apiculata* differs from *S. pachycarpa* in having abruptly acuminate leaves.

3. *Sphaerotheciella pinnata* (Schimp. *in* B.S.G.) Manuel, Occas. Pap. Farlow Herb. Cryptog. Bot. 12: 36. 1977. *Cryphaea pinnata* Schimp. *in* B.S.G., Bryol. Eur. 5: 35. 1850 (fasc. 44–45). Protologue. *Professor Liebmann* in Mexiko gesammelt und uns mitgetheilt. Type (see Manuel 1977b). Mexico. *S. loc.*, *Liebmann, s.n.* (BM, lectotype).

Plants medium-sized, in green or yellow green mats. Primary stems creeping, irregularly branched; rhizoids from clusters of initials abaxial to the leaf insertions, red, smooth, unbranched or rarely irregularly branched. Secondary stems horizontal or erect and loosely spreading, to 10 cm long, irregularly branched; cross section with sclerodermis of 3–6 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, very thick-walled, central strand absent; paraphyllia absent;

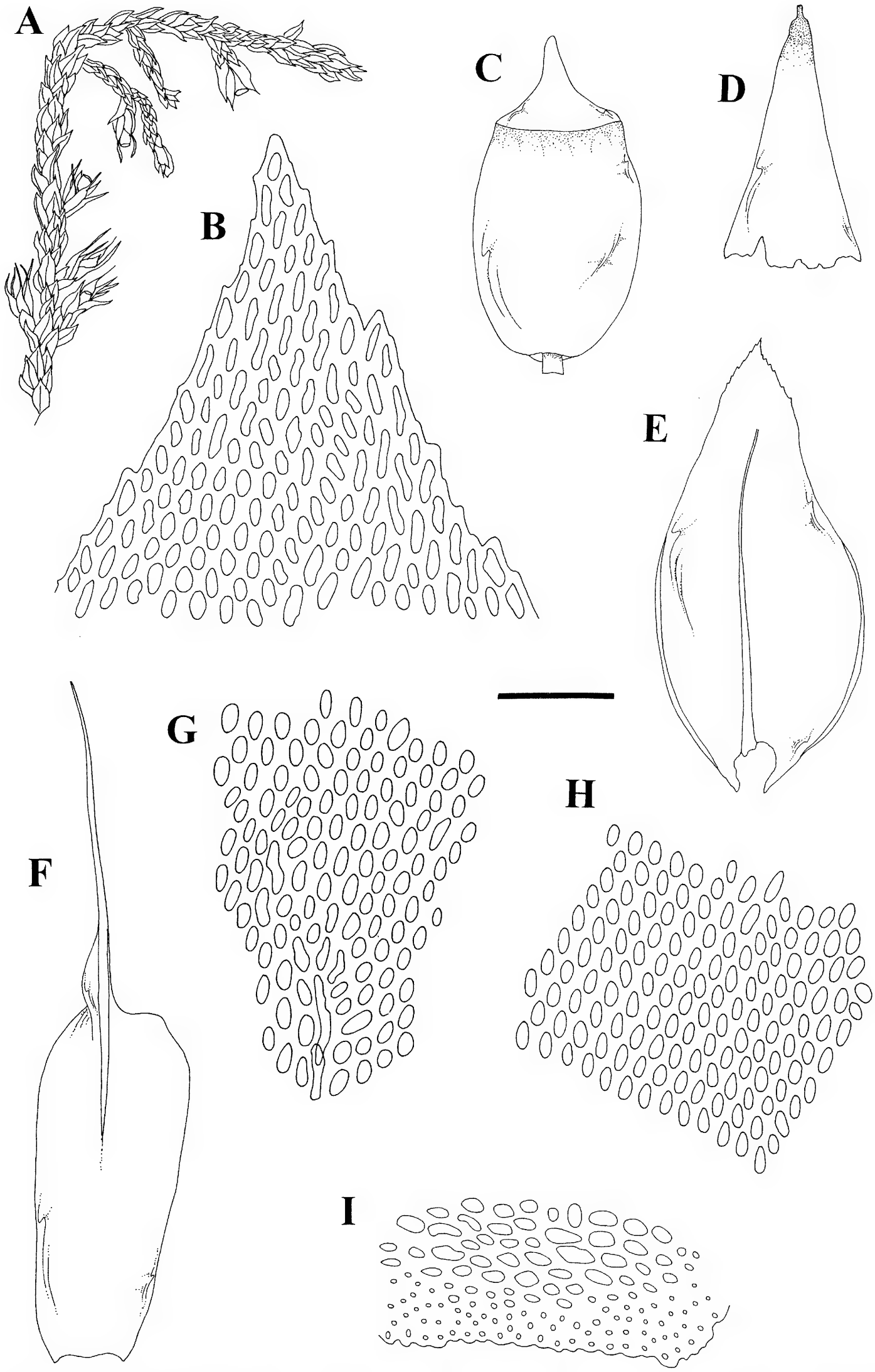
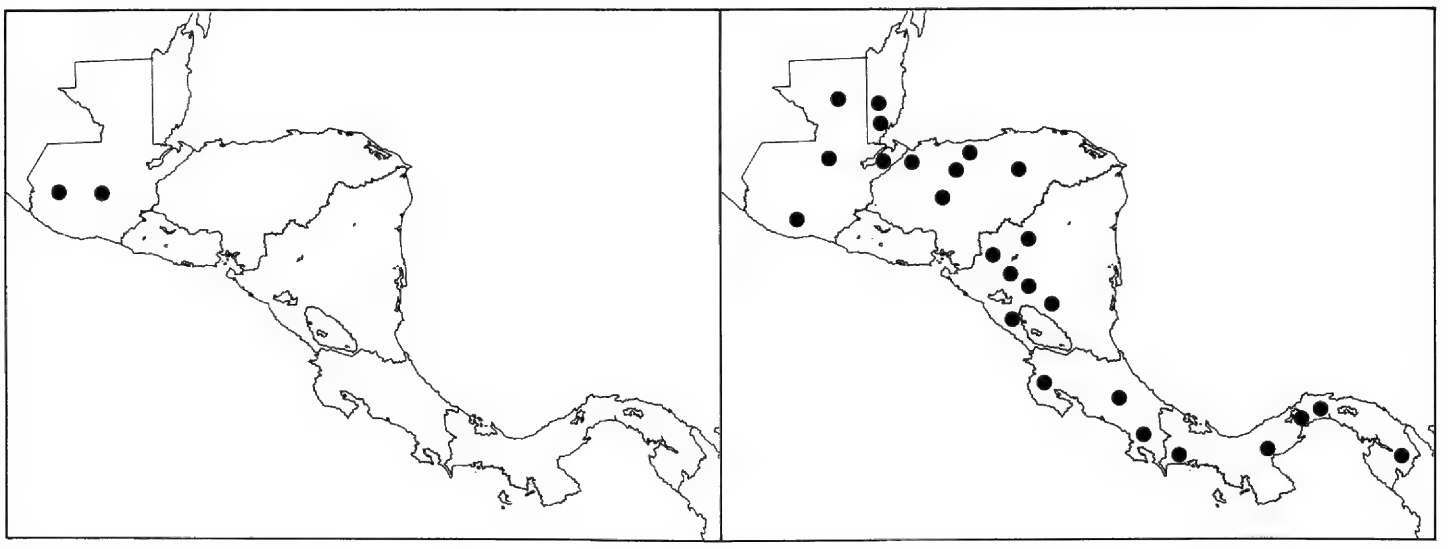


Figure 25. *Sphaerotheciella pinnata*. A. Habit. B. Leaf apex. C. Seta and capsule. D. Calyptra. E. Leaf. F. Perichaetial leaf. G. Median cells above the costa. H. Upper leaf cells. I. Stem in cross section. Scale in mm: bar = 0.05 (B, G, H); bar = 0.06 (I); bar = 0.26 (D); bar = 0.5 (F); bar = 0.6 (C, E); bar = 4.0 (A). A, C, D, F from *Pringle 15047*; all other figure parts from *Sharp 5037*.



Sphaerotheciella pinnata *Pseudocryphaea domingensis*

pseudoparaphyllia filamentous or subfoliose and with scale leaves. Secondary stem and branch leaves ovate-lanceolate, 1.2–2.4 mm long, imbricate to loosely imbricate, at times wrinkled when dry, spreading when wet, gradually acuminate, decurrent; margins revolute in lower 3/4 or less, serrate to denticulate above; costae strong, 0.7–0.8 the leaf length; cells smooth and thick-walled, cells in apex fusiform, upper cells narrowly elliptic, 13–26 µm long, median cells elliptic, 10–20 µm long; basal cells near costa in lower 1/6 of leaf elongate to linear, to 40 µm long; alar cells short-rectangular, subquadrate, or oblate, 6–16 µm. Autoicous. Perichaetia and perigonia lateral. Perigonial leaves ovate, ecostate; perichaetial leaves oblong, inner ones abruptly narrowed to a long, smooth or lightly roughened awn equal to or somewhat shorter than the leaf lamina, costae discontinuous, stoutly filling the apex, absent at base. Setae short, 0.1–0.2 µm long, cells quadrate. Capsules immersed, ellipsoid, 1.0–1.5 mm long, smooth, light brown, narrowed at the mouth, abruptly rounded-indented to the setae; exothecial cells small, red, in 2–3 rows below the mouth, irregularly short-rectangular below; stomata not seen; opercula conic-rostrate, smooth, to 0.5 mm long; annuli compound; peristome diplolepideous, inserted within the mouth; exostome teeth narrowly triangular to linear, whitish yellow, dorsal (outer) surface smooth below, papillose above, to 0.40 mm long; endostome segments linear, papillose, shorter than the exostome, cilia absent, basal membranes very low. Spores massive, spherical or irregularly oblong, lightly papillose, 40–60 µm. Spores endosporically germinated within the capsule. Calyptrae mitrate, smooth, 0.4–0.6 mm long.

Illustrations. Manuel (1977b, Figs. 2–10); Sharp *et al.* (1994, Fig. 516 d–f); Gradstein *et al.* (2001, Fig. 105 A–E). Figure 25.

Habitat. On tree trunks and branches (*Alnus*), occasionally on non-calcareous boulders; 2590–3048 m.

Distribution in Central America. GUATEMALA. Guatemala: *Standley 80654* (F); Quetzaltenango: *Sharp 5037* (FH, TENN).

World range: Mexico; Central America; Northern South America.

Sphaerotheciella pinnata has ovate-lanceolate, acuminate leaves with serrate to denticulate upper margins, and fusiform to elongate cells in the extreme apex. These features distinguish it from *S. pachycarpa* which has ovate, acute to broadly acuminate leaves with entire to crenulate upper margins, and oval to elliptic cells in the extreme apex. As noted by Manuel (1977b), apical leaf cell form in *S. pinnata* appears to be correlated with leaf apex shape. Plants with abruptly narrowed leaves have longer, narrower leaf cells than those with gradually narrowed leaf apices. Both *S. pinnata* and *S. gracillima* have ovate-lanceolate leaves and long apical leaf cells. The leaves of *S. gracillima*, however, are narrower, more abruptly acuminate than those of *S. pinnata*, and its upper leaf margins are entire to crenulate.

The gametophytes of *Cryphaea patens* are so similar to those of *S. pinnata* that, lacking sporophytes, the two species often cannot be distinguished without the benefit of comparative material. In *C. patens* the costae are somewhat longer (0.8–0.9 vs. 0.6–0.8 the leaf length) than those of *S. pinnata* and they are often wavy above, while the costae of *S. pinnata* are straight. In addition, *C. patens* has elongate leaf cells from the tip of the costa to the leaf apex, while those of *S. pinnata* are elliptic. This last feature must be carefully evaluated since the extreme apical leaf cells in *S. pinnata* are fusiform to elongate. The report of *S. pinnata* from Costa Rica (Manuel 1981) is based on a collection of *S. gracillima*.

FORSSTROEMIACEAE

Forsstroemiaceae B. H. Allen, *stat. et comb. nov.* Basionym: Leucodontaceae Schimp. subfam. Forsstroemioideae Manuel, Bryol. 77: 535. 1974.

Plants dendroid. Primary stems creeping, with reduced leaves. Secondary stems erect, irregularly branched; cross section with central strand absent; paraphyllia absent; pseudoparaphyllia filamentous to irregularly foliose; rhizoids red, smooth, not or weakly branched, from circular clusters of initials abaxial to the stolon leaf insertions. Leaf costae single, short and double or absent; median cells elliptic to linear; alar cells quadrate to oblate. Dioicous or autoicous. Setae immersed or exserted. Exostome teeth 16, smooth to minutely papillose; endostome segments rudimentary to absent, cilia absent. Calyptrae cucullate.

1. *Pseudocryphaea* E. Britton *ex* Broth., Nat. Pflanzenfam. (ed. 2) 11: 98. 1925.

Pseudocryphaea E. Britton, Bull. Torrey Bot. Club 32: 261. 1905, *nom. nud.*

Plants epiphytic, occasionally saxicolous, in thin or dense wefts. Primary stems creeping, with reduced leaves. Secondary stems erect, irregularly branched; cross section with enlarged but thick-walled outer layer of reddish cells, several rows of small, thick-walled reddish subepidermal cells, enlarged cortical cells, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous to irregularly foliose; rhizoids red, smooth, not or weakly branched, from circular clusters of initials abaxial to the stolon leaf insertions; axillary hairs with 1–2 short red brown basal cells, 4–8 oblate, red brown cells, and a single hyaline (often granulose) elongate, terminal cell. Stem leaves ovate, acuminate, lowermost leaves ecostate, median and upper leaves with single, strong costae. Branch leaves ovate-lanceolate to lanceolate, erect-appressed to erect-spreading when dry, spreading when wet, gradually acuminate, short-decurrent; margins plane to erect, subentire to serrulate above, entire below; costae single, percurrent to subpercurrent, in cross section with two rows of homogeneous cells; cells minutely prorate, firm-walled, apical and median cells linear, fusiform, or long-hexagonal, not porose; basal cells long-fusiform to prosenchymatous, often porose; alar cells quadrate to oblate, collenchymatous, cells across the insertions reddish yellow. Asexual reproduction by deciduous, microphyllous branchlets. Dioicous. Perichaetia lateral, gemmate, sessile on branches; leaves lanceolate-acuminate, ecostate; paraphyses present; archegonia numerous. Perigonia and sporophytes not seen.

Pseudocryphaea is a monospecific genus found only in the New World from Florida, U.S.A., to Paraguay. Although predominantly corticolous, the genus occasionally occurs on rocks. Müller (1850) described the genus as having long, slender, yellow setae and erect, ovate capsules, but did not mention its peristome. No one has since seen the sporophytes of *Pseudocryphaea*, and, according to Buck (1980), Fleischer indicated there were no fertile collections of *Pseudocryphaea* in the Müller herbarium. The systematic placement of *Pseudocryphaea* is based entirely on gametophytic evidence, and as a result its position is uncertain. Plants of *Pseudocryphaea* are dendroid, with sympodially branched stolons that are appressed to the substrate and rhizoids more or less restricted to the stolons. The erect secondary stems are irregularly pinnately branched, and the branches commonly have axillary, microphyllous branchlets. The stolon, lowermost stem, and microphyllous branchlet leaves are ecostate; otherwise the leaves have long, single, usually percurrent costae that consist of only two layers of cells. The leaves of *Pseudocryphaea* have extensively developed quadrate to oblate alar cells and long, often linear-fusiform, weakly prorate leaf cells. Other noteworthy features of the genus include stems with somewhat enlarged epidermal cells, filamentous to subfoliose and incised pseudoparaphyllia, and axillary hairs that have 4–8 oblate intercalary cells.

Pseudocryphaea has been associated with the Leucodontaceae (Brotherus 1925; Bartram 1949; Florschütz 1964; Manuel 1974; Crum & Anderson 1981; Vitt 1984), Rutenbergiaceae (Buck *et al.* 2000a, 2000b; Buck & Goffinet 2000), and Leptodontaceae (Buck 1980; Buck & Vitt 1986; Buck 1998). All these families have plants with sympodial branched, creeping stolons that are adnate to the substrate, and rhizoids that are restricted to the stolons. A positioning of *Pseudocryphaea* in the Leu-

codontaceae appears unlikely since that family is characterized by short leaf cells and ecostate leaves. In morphological terms the placement of *Pseudocryphaea* in the Rutenbergiaceae is unsupportable. *Pseudocryphaea* was placed in that family solely on molecular evidence from two chloroplast loci. In addition to the lack of morphological evidence supporting this placement of the genus, the molecular evidence placing it in the Rutenbergiaceae is weak: the Bremer support index for the analysis was "low or completely lacking" and "Jackknifing and bootstrap values were in all cases below 60%" (Buck *et al.* 2000b).

The Leptodontaceae also do not appear to be a proper placement for *Pseudocryphaea*, because the type genus has scattered paraphyllia and leaves with short, rounded leaf cells and strong single costae. Indeed, *Leptodon* appears closer to the Neckeraceae than either the Cryphaeaceae or Leucodontaceae. *Forsstroemia* Lindb., which is sometimes placed in the Leptodontaceae, is very similar to *Pseudocryphaea* in several features. In addition to the generalized features noted above, the secondary stems in these genera lack paraphyllia, have identical pseudoparaphyllia, and a similar branching pattern. Also some species of *Forsstroemia* have leaves that are appressed to imbricate when dry, a similar areolation, and weak, variable costae. Even the microphyllous branchlets of *Pseudocryphaea* have a counterpart in the propaguliferous branchlets of *F. japonica* (Besch.) Paris. *Forsstroemia* differs from *Pseudocryphaea* only in having small stem epidermal cells and axillary hairs that lack oblate intercalary cells. Manuel (1974) was the first to suggest a relationship between *Forsstroemia* and *Pseudocryphaea* when he placed them along with *Henicodium* in the Forsstroemioideae. *Henicodium* belongs in the Pterobryaceae. *Forsstroemia* and *Pseudocryphaea* are treated here as the only members of the Forsstroemiaceae.

The name *Pseudocryphaea* combines the Greek *pseudo* (false) with the generic name *Cryphaea*.

Pseudocryphaea domingensis (Spreng.) W. R. Buck, Bryologist 83: 455. 1980 [1981]. *Neckera domingensis* Spreng., Syst. Veg. 4(1): 185. 1827. *Leucodon domingensis* (Spreng.) Mitt., J. Linn. Soc., Bot. 12: 409. 1869. *Pterigynandrum domingense* (Spreng.) Hampe, Vidensk. Meddel. Dansk. Naturhist. Foren Kjøbenhavn IV 1: 129. 1879. Protologue. Hispanola. *Bertero.*

Pilotrichum flagelliferum Brid., Bryol. Univ. 2: 259. 1827, illegitimate name, includes an earlier name. *Leucodon flagellaris* Bertero *ex* Brid., Bryol. Univ. 2: 259. 1827, invalid name, lacks a description. *Pseudocryphaea flagellifera* (Brid.) E. Britton, Bull. Torrey Bot. Club 32: 261. 1905, invalid combination. *Pseudocryphaea flagellifera* (Brid.) E. Britton *ex* Broth., Nat. Pflanzenfam. (ed. 2) 11: 98. 1925. Protologue. In Hispanioâ et Puerto Ricco, ubi *Bertero* detexit, habitat, arborum cortici adrepens. Herb. Candol.
Cryphaea leptoclada Sull., Proc. Amer. Acad. Arts. 5: 283. 1861. Protologue. Cuba, *Wright 68.*

Plants medium-sized to robust, in green, yellow green or yellowish brown, epiphytic, occasionally saxicolous, dendroid, wefts. Primary stems creeping; leaves reduced, ovate-acuminate, scale-like, ecostate. Secondary stems erect, irregularly pinnately branched, to 9 cm long; cross section with enlarged but thick-walled outer layer of reddish cells, 4–6 rows of small, thick-walled reddish cells, cortical cells somewhat enlarged, yellow to hyaline, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous to irregularly foliose, often incised; rhizoids red, smooth, not or weakly branched, from circular clusters of initials at abaxial side of stolon leaf insertions; axillary hairs with 1–2 short, red brown basal cells, 4–8 oblate, red brown intercalary cells, and a single hyaline (often granulose) elongate, terminal cell. Stem leaves ovate, acuminate, 1–2 mm long, lowermost leaves ecostate, median and upper leaves with single strong costae. Branches to 20 mm long. Branch leaves ovate-lanceolate to lanceolate, 1–2 mm long, erect-appressed to erect-spreading when dry, spreading when wet, gradually acuminate, short-decurrent; margins plane to erect, subentire to serrulate above, entire below; costae single, percurrent to subpercurrent, in cross section with two rows of homogeneous cells; cells minutely prorate, firm-walled, apical and median cells linear, fusiform to long-hexagonal, not porose, 35–50 × 6–7 µm; basal cells long-fusiform to prosenchymatous, often porose, 60–90 × 6–7 µm; alar cells quadrate to oblate, collenchymatous, cells across the insertion reddish yellow. Asexual reproduction by deciduous, microphyllous branchlets, 4–5 mm long; leaves 0.2 mm long, ecostate; alar cells weakly developed. Dioicous. Perichaetia gemmate, 1–1.5 mm long, sessile on branches; leaves lanceolate-acuminate, ecostate; paraphyses present; archegonia numerous. Perigonia and sporophytes not seen.

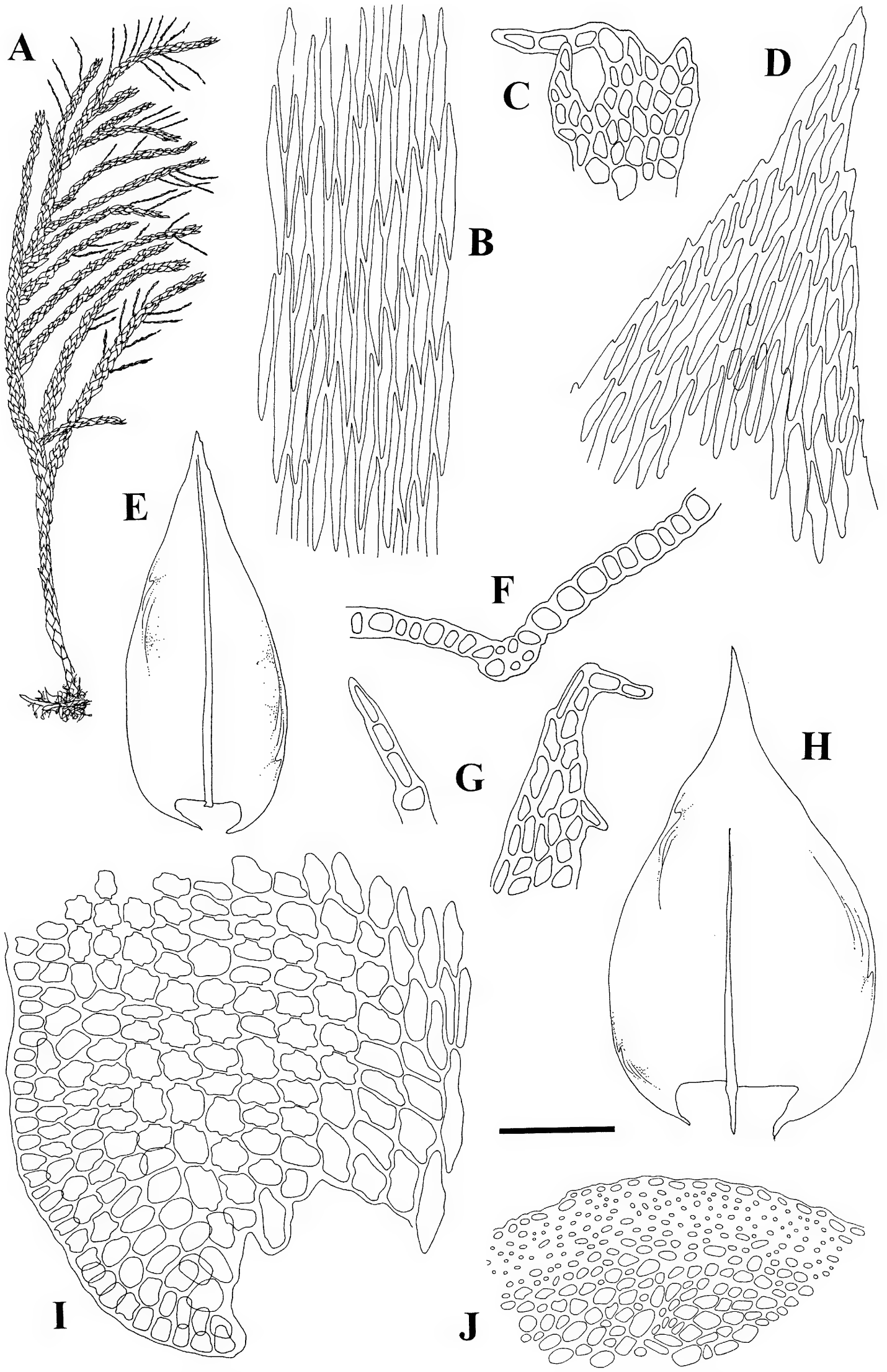


Figure 26. *Pseudocryphaea domingensis*. A. Habit. B. Median leaf cells. C & G. Pseudoparaphyllia. D. Leaf apex. E. Branch leaf. F. Leaf in cross section. H. Stem leaf. I. Leaf alar region. J. Stem in cross section. Scale in mm: bar = 0.05 (C, F, G); bar = 0.06 (B, D, I); bar = 0.08 (J); bar = 0.5 (E, H); bar = 6.4 (A). All figure parts from *Allen 18106*.

Illustrations. Bartram (1949, Fig. 110 C–E); Florschütz (1964, Fig. 97); Sharp *et al.* (1994, Fig. 503); Churchill and Linares (1995, Fig. 113 a–e); Duarte Bello (1997, Pl. 177); Buck (1998, Pl. 63 Figs. 9–15); Gradstein *et al.* (2001, Fig. 144 I–N). Figure 26.

Habitat. On tree trunks, branches, rotting logs, vines, and twigs, occasionally on sides of boulders; 50–1676 m.

Distribution in Central America. BELIZE. Cayo: *Allen 18202* (BRM, MO); Toledo: *Davidse & Brant 32417A* (MO). GUATEMALA. Alta Verapaz: *Johnson 444* (US); Escuintla: *Aguilar 1720* (F, FH, NY); Izabal: *Standley* 72518a (FH); Petén: *Morgan 8* (MO). EL SALVADOR. Santa Ana: *Sipman 37382* (NY). HONDURAS. Atlántida: *Allen 17649* (MO, TEFH); Comayagua: *Allen 13738* (MO, TEFH); Cortés: *Morton 7878* (US); Olancho: *Allen 12431* (MO, TEFH); Yoro: *Allen 13510* (MO, TEFH). NICARAGUA. Boaco: *Stevens 14639* (HNMN, MO); Chontales: *Stevens 2860A* (MO); Granada: *Moreno 431* (MO); Jinotega: *Croat 42943* (HNMN, MO); Madriz: *Stevens 16142* (HNMN, MO); Matagalpa: *Guzmán & Castro 1623B* (HNMN, MO). COSTA RICA. Cartago: *Richards 6283* (MO); Guanacaste: *Standley & Valerio 46658* (FH, US); Puntarenas: *Zúñiga 262* (MO). PANAMA. Canal Area: *Dodge et al. 181035* (MO); Chiriquí: *Busey* 587 (FH, MO); Coclé: *Cornman 3024B* (MO); Darién: *Allen 8647* (MO, PMA); Panamá: *Gentry 5602* (MO).

World range: Southeastern U.S.A.; Mexico; Central America; Caribbean; Western, Northern, and Southern South America, Brazil.

Pseudocryphaea domingensis is a large, dendroid moss usually found on tree trunks and branches. Wet plants of *P. domingensis* have strongly spreading leaves, but when dry the leaves are typically erect-appressed and the branches are distinctly curved. The dry leaves of *P. domingensis*, however, are remarkably variable in stance, and some plants have erect-spreading leaves that give them a much different aspect than those with appressed leaves. There are, in addition, collections of *P. domingensis* that have plants with both types of leaf stance.

The presence of numerous long, axillary, microphyllous branchlets on the stems and branches of *P. domingensis* is the most distinctive feature of the species. These branchlets appear to arise from branch primordia rather than single cells, they have reduced scale leaves at base, and Florschütz (1964) reported they sometimes are "radiculose at base." The axillary hairs of *P. domingensis* are an especially odd feature of the species. They have 1–2 reddish brown, normally shaped basal cells and an elongate, hyaline terminal cell, but in between there are 4–8 reddish brown, oblate cells. The numerous red brown cells in the axillary hairs make them easy to see. Their morphology is so distinctive that it can be effectively used to identify depauperate collections that lack microphyllous branchlets. Additional distinctive features of the species include the presence of stolons with scale-like leaves; stem and branch leaves with long, single costae; fusiform to prosenchymatous leaf cells that are faintly prorate; and numerous quadrate to oblate alar cells.

Pseudocryphaea domingensis is sometimes be confused with *Henicodium geniculatum.* Plants of *H. geniculatum*, however, never have microphyllous axillary branchlets. Furthermore, their leaves have recurved margins, cells with papillae over lumina, costae that consistently end below the apex, and 4-celled axillary hairs with two short, brown basal cells and two elongate, hyaline apical cells.

LEUCODONTACEAE

Leucodontaceae Schimp., Coroll. Bryol. Eur. 108. 1856.

Plants slender to robust in dense, usually epiphytic mats. Primary stems creeping. Secondary stems horizontal or erect, irregularly branched; cross section with sclerodermis, firm-walled cortex, central strand present or absent; paraphyllia absent; pseudoparaphyllia present or absent, scale leaves present; rhizoids from circular clusters of initials abaxial to the leaf insertions. Leaves ovate-lanceolate, smooth or plicate, often secund when dry, acute or acuminate, slightly decurrent; margins plane or recurved at base; costa absent; cells smooth, occasionally mammillose to prorate, sometimes porose, thick-walled, apical and median cells linear to fusiform; basal median cells linear, often porose; alar cells quadrate to oblate. Dioicous. Perichaetial leaves convolute-sheathing. Setae elongate. Capsules immersed, emergent or variously exserted, subglobose, oblong-ellipsoid, or cylindrical, smooth or furrowed when dry; stomata present or absent; opercula rostrate to obliquely rostrate; annuli rudimentary, cells clinging to the operculum base and capsule mouth after dehiscence; peristome diplolepideous, properistome at times well developed; exostome teeth narrowly triangular, at times chambered, yellowish white, variously papillose; endostome basal membranes low, pale, lightly papillose, segments and cilia absent, rarely with a high basal membrane and low segments. Spores small and round or large and irregularly oblong, exosporically or endosporically germinated. Calyptrae cucullate, smooth, naked.

The circumscription of the Leucodontaceae is unsettled, and there are many different opinions on the limits of the family (see, *e.g.*, Fleischer 1908; Brotherus 1925; Manuel 1974; Akiyama 1994; Buck 1980, 1998; Buck & Goffinet 2000; Goffinet & Buck 2004). The number of genera placed in the family varies from eleven (Manuel 1974; Walther 1983) to two (Buck 1998). According to Akiyama (1994), establishing morphological limits for the Leucodontaceae is a daunting task because most of the pertinent genera are monospecific, and, since all the genera are epiphytic, character convergence is likely to be high. As treated here the circumscription of Leucodontaceae is narrow and, following Buck (1998) and Akiyama (1994), includes three genera: *Leucodon* Schwägr. (39 species), *Leucodontella* Nog. (1 species), and *Pterogoniadelphus* M. Fleisch. (= *Felipponea*; 3 species). The three genera are exceedingly close; Akiyama (1988, 1994) in fact treats *Leucodontella* as a subgenus of *Leucodon*.

Members of the Leucodontaceae have creeping stolons with erect or pendent secondary stems that lack paraphyllia. The stolons and stems may or may not have internal differentiation, and pseudoparaphyllia can be present or absent. The rhizoids are nearly unbranched and generally come from circular clusters of initials abaxial to the leaf insertions. The leaves are ecostate. The leaf cells are thick-walled, usually smooth, and the basal cells in the alar region are quadrate to oblate. Members of the Leucodontaceae are dioicous, and they often have strongly differentiated perichaetial leaves, immersed, emergent or long-exserted capsules, reduced peristomes, and cucullate calyptrae. The peristomes of *Leucodontella* and *Pterogoniadelphus* lack prostomial development, and this feature is also lacking in some species of *Leucodon*. *Leucodontella* is distinguished from the other members of the family by its endostomial morphology: high basal membrane and short segments. *Pterogoniadelphus* differs from *Leucodon* only in having more extensively developed alar cells.

1. *Leucodon* Schwägr., Sp. Musc. Frond. Suppl. 1(2): 1. 1816. *Neckera* sect. *Leucodon* (Schwaegr.) Müll. Hal., Syn. Musc. Frond. 2: 91. 1850.

Plants slender, medium-sized, or robust. Primary stems creeping. Secondary stems horizontal or erect, irregularly branched; cross section with sclerodermis, firm-walled cortex, central strand present or absent; paraphyllia absent; pseudoparaphyllia absent, scale leaves present; rhizoids from circular clusters of initials abaxial to the leaf insertions. Leaves ovate-lanceolate, smooth or plicate, erect or spreading, often secund when dry, acuminate, decurrent; margins plane or recurved at base; costa absent; cells smooth, thick-walled, apical and median cells linear to fusiform; basal median cells linear, often porose; alar cells quadrate to oblate. Dioicous. Perichaetial leaves convolute-sheathing. Setae elongate. Capsules immersed, emergent, or variously exserted, subglobose to oblong-ellipsoid,

2–3 mm long, smooth or irregularly furrowed when dry, narrowed at the mouth; exothecial cells small, red, very thick-walled in several rows below the mouth, firm-walled, irregularly short-rectangular below; stomata present or absent; opercula rostrate to obliquely rostrate; annuli rudimentary, cells clinging to the operculum base and capsule mouth after dehiscence; peristome diplolepideous, prostome at times well developed; exostome teeth narrowly triangular, yellowish white, variously papillose; endostome basal membrane very low, pale, lightly papillose, segments and cilia absent. Spores finely papillose, small and round or large and irregularly oblong, exosporically or endosporically germinated. Calyptrae cucullate, smooth, naked.

Leucodon, a genus of 39 species (Crosby *et al.* 2000), is absent from Australasia but otherwise found throughout the world. The genus is predominantly corticolous, but it also occurs on rocks, and a few *Leucodon* species grow mostly on calcareous rocks. There are 20 species of *Leucodon* in eastern Asia, and this area appears to be its center of diversity. In terms of morphological variation, *Leucodon* in eastern Asia is especially noteworthy, *e.g.*, Central American species of *Leucodon* lack a stem central strand and properistomial development, but some East Asian species of *Leucodon* have a stem central strand and extensively developed (sometimes chambered) properistomes.

Plants of *Leucodon* have four more or less distinct parts: stolons appressed to the substrate, simple or irregularly branched secondary stems at more or less right angles to the stolons, flagellate branchlets, and pendent shoots. The genus has absolutely ecostate leaves and smooth, firm-walled leaf cells. The leaves typically have elongate cells in the basal median region and numerous quadrate to oblate alar cells. *Leucodon* is a dioicous genus with smooth, cucullate calyptrae and sheathing perichaetial leaves. The peristome in *Leucodon* consists of whitish yellow, narrowly triangular, and variously papillose exostome teeth and an endostome reduced to a short basal membrane.

The annulus in *L. brachypus* consists of several rows of small, thick-walled cells. Dehiscence occurs along an irregular line of weakness, and the annular cells are persistent, remaining attached to both the operculum and the capsule mouth. Akiyama (1988) characterized the annulus in *Leucodon* as "clearly differentiated." Buck (1998), however, considered it absent because it was not a deciduous structure. I agree with Akiyama that an annulus is a structure that facilitates the separation of the operculum from the capsule along a distinct line.

The eastern Asian species of *Leucodon* were revised by Akiyama (1988). This treatment gives a detailed morphological analysis of the genus and divides the genus into three subgenera (*Leucodon*, *Leucodontella* (Nog.) Nog., and *Cryptotheca* Akiyama). Subgenus *Leucodon* is further divided into two sections (*Leucodon* and *Macrosporiella* (Dixon & Thér.) Akiyama).

The name *Leucodon* combines the Greek *leucon* (white) with *odontos* (tooth) and refers to the whitish yellow peristome found in the genus.

1. Plants slender; leaves acute to abruptly short-acuminate, 1.6–2.2 mm long; apical leaf cells mostly or entirely oblong; capsules immersed or laterally emergent . . . . . 1. *L. brachypus*
1. Plants medium-sized to robust; leaves narrowly acuminate, 2.3–3.5 mm long; apical leaf cells mostly or entirely linear; capsules emergent to long-exserted . . . . . 2. *L. curvirostris*

1. *Leucodon brachypus* Brid., Bryol. Univ. 2: 210. 1827. *Leucodontella brachypus* (Brid.) Nog., J. Hattori Bot. Lab. 2: 40. 1947. Protologue. [United States] In Americae Foederatae Provinciâ Massachusets in arboribus vivit. *D.* Torrey Noveboraco misit.

Plants slender to medium-sized, in green, yellow green, or yellowish brown mats. Primary stems creeping. Secondary stems horizontal or erect, irregularly branched, to 5 cm long; cross section with sclerodermis of 3–5 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent, scale leaves present; rhizoids red, smooth, not or weakly branched, from circular clusters of initials abaxial to the leaf insertions, at times extending onto the leaf base. Stem and branch leaves differing only in size. Leaves ovate-lanceolate, plicate, 1.6–2.2 mm long, erect to erect-secund when dry, erect-spreading when wet, acute or abruptly short-acuminate, decurrent; margins recurved in lower 1/2, sometimes plane, entire to lightly serrulate above; costa absent; cells smooth, thick-walled, apical and median cells linear, fusiform or oval, 14–40 × 5–6 μm; basal median cells linear, to 80 × 3 μm; alar cells

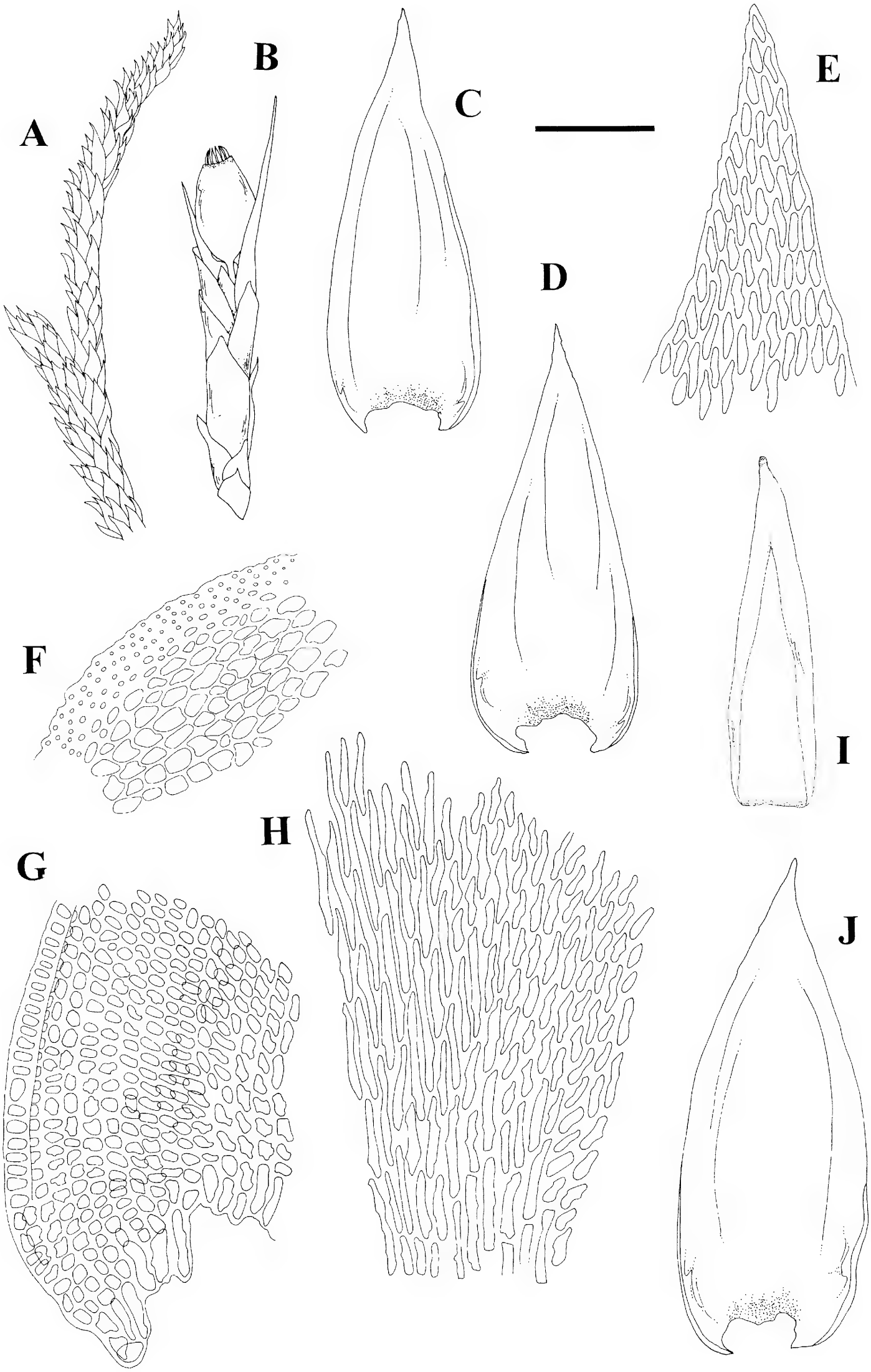
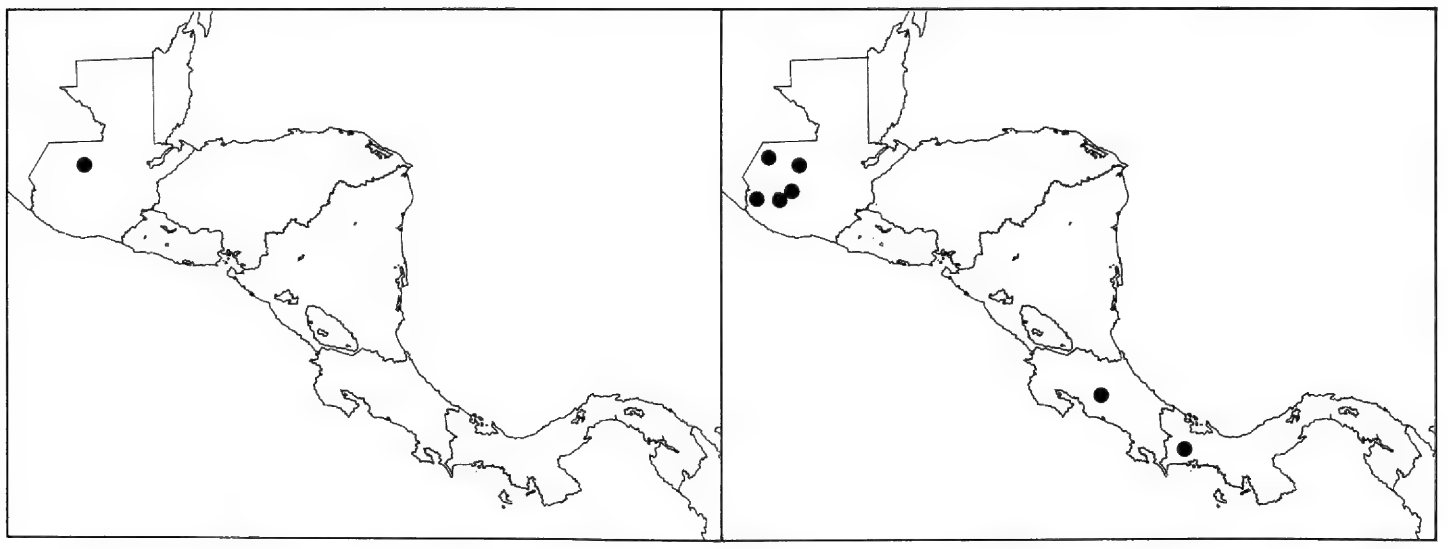


Figure 27. *Leucodon brachypus*. A. Habit. B. Sporophyte. C, D & J. Leaves. E. Leaf apex. F. Stem in cross section. G. Leaf alar region. H. Leaf basal cells near costa. I. Calyptra. Scale in mm: bar = 0.06 (E, G, H); bar = 0.08 (F); bar = 0.71 (C, D, J); bar = 1.3 (I); bar = 1.56 (B); bar = 2.5 (A). B from *Pursell 3873*; I from *Reese 5387*; all other figure parts from *Richards 3081*.



Leucodon brachypus *Leucodon curvirostris*

quadrate to oblate. Dioicous. Perichaetial leaves convolute-sheathing, exceeding the capsules, 4–6 mm long. Setae 2–4 mm long, dark red. Capsules immersed or laterally emergent, oblong-ellipsoid, 1.2–2.0 mm long, smooth or irregularly furrowed when dry, narrowed at the mouth, red brown; exothecial cells small, red, very thick-walled in 3–5 rows below the mouth, firm-walled, irregularly short-rectangular below; stomata absent; opercula rostrate to obliquely rostrate, red, 1.0 mm long; annuli rudimentary, cells clinging to the operculum base and capsule mouth after dehiscence; peristome diplolepideous; exostome teeth narrowly triangular, whitish, densely papillose, to 0.25 mm long; endostome basal membranes low, pale, lightly papillose, segments and cilia absent. Spores round, irregularly rounded, or oblong, finely papillose, 30–54 µm, exosporically germinated. Calyptrae cucullate, yellowish, smooth, naked, 2.0–2.5 mm long.

Illustrations. Sullivant (1864, Pl. 70); Grout (1910, Fig. 212 c & k, Fig. 213 a–c); Jennings (1951, Pl. 35); Crum and Anderson (1981, Fig. 364); Ireland (1982, Pl. 234). Figure 27.

Habitat. On bark at base of trees; 2000 m.

Distribution in Central America. GUATEMALA. Quiché: *Richards 3081* (F, FH).

World range: Eastern Canada, North-Central, Northeastern, Southwestern, South-Central, and Southeastern U.S.A.; Mexico; Central America.

Although the Central American species of *Leucodon* have variously falcate-secund, plicate leaves, *L. brachypus* is a smaller plant than *L. curvirostris* and its leaves are generally more stiffly erect-secund when dry. *Leucodon curvirostris*, however, is remarkably variable in both gametophytic and sporophytic features. Most collections of *L. curvirostris* have leaves greater than 2.5 mm long and a much laxer aspect than *L. brachypus*, but there are some collections with erect leaves that are only 2.3 mm long. These collections can be distinguished from *L. brachypus* by their narrowly acuminate leaf apices and predominantly linear apical cells. *Leucodon curvirostris* further differs from *L. brachypus* in having exserted capsules. The setae in *L. curvirostris*, however, are distressingly variable and sometimes the capsules are merely emergent.

In size *L. brachypus* is similar to *L. julaceus*, which is present in eastern Mexico. *Leucodon julaceus* differs from *L. brachypus* in having julaceous stems, shorter (1.1–1.6 mm vs. 1.6–2.2 mm), non-plicate leaves that are appressed when dry, and shortly exserted capsules. This is the first report of *L. brachypus* from Mexico. The species occurs in the Mexican states of Tamaulipas (*Reese 5387*, c.fr., MO) and Nuevo León (*Sharp 3903*, US).

2. *Leucodon curvirostris* Hampe, Icones Musc. 16. 1844. *Astrodontium curvirostris* (Hampe) Schimp. *ex* Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 218. 1872. Protologue. E Mexico relatus et mecum communicatus, nec loco natali, nec inventore indicatis.

Leucodon macrosporus R. S. Williams, Contr. U. S. Natl. Herb. 16: 23. 1912. Protologue. Vicinity of Camp Aguacatal, eastern slope of Chiriquí Volcano, Chiriquí, Panama, altitude 2100–2300 meters, March 10 to

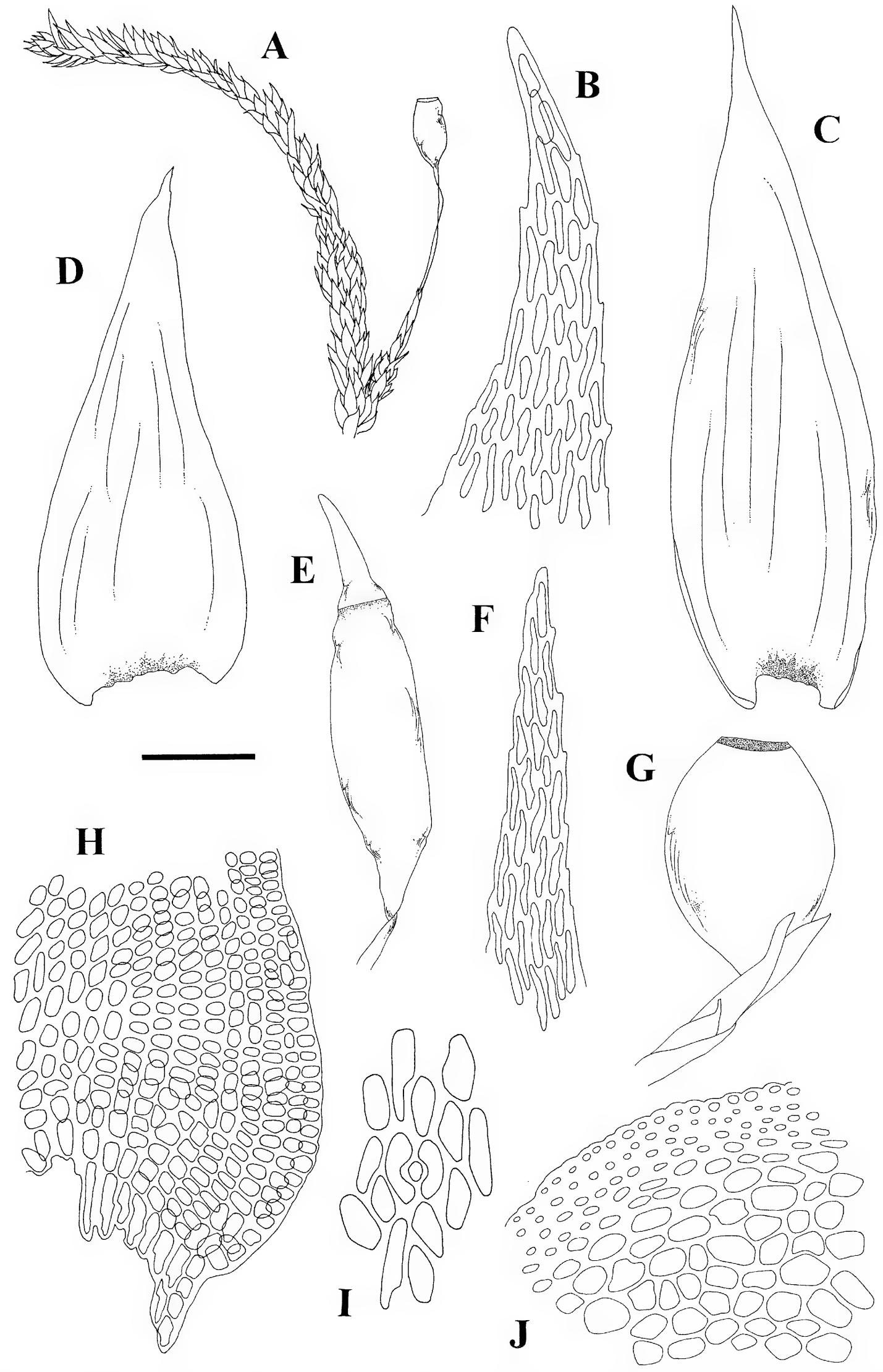


Figure 28. *Leucodon curvirostris*. A. Habit. B & F. Leaf apices. C & D. Leaves. E. Seta, capsule, and operculum. G. Capsule. H. Leaf alar region. I. Stomata. J. Stem in cross section. Scale in mm: bar = 0.05 (I); bar = 0.06 (B, F, H); bar = 0.08 (J); bar = 0.6 (C, D); bar = 1.3 (E, G); bar = 5.1 (A). E, I from *Sharp 2088*; G from *Sharp 5050*; all other figure parts from *Crosby & Crosby 5737*.

13, 1911, *Maxon 5276*. Type. Vicinity of Camp Aguacatal, eastern slope of Chiriquí Volcano, Chiriquí, Panama, altitude 2100 to 2300 meters, March 10 to 13, 1911, *Maxon 5276* (US, isotype).

Plants medium-sized to robust, in green, yellow green, or yellowish brown mats. Primary stems creeping. Secondary stems horizontal or erect, irregularly branched, to 10 cm long; cross section with sclerodermis of 3–5 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent, scale leaves present; rhizoids red, smooth, not or weakly branched, from circular clusters of initials abaxial to the leaf insertions. Stem and branch leaves differing only in size. Leaves ovate-lanceolate, plicate, 2.3–3.6 mm long, erect or spreading, often secund when dry, erect-spreading when wet, narrowly acuminate, decurrent; margins plane or recurved in lower 1/4, lightly serrulate above; costa absent; cells smooth, thick-walled, apical and median cells linear to fusiform, 16–30 × 4–6 µm; basal median cells linear, often porose, to 80 × 6 µm; alar cells quadrate to oblate. Dioicous. Perichaetial leaves convolute-sheathing, at times reaching the base of the capsules, 3–7 mm long. Setae 4–12 mm long, dark red. Capsules emergent to long-exserted, subglobose to oblong-ellipsoid, 2–3 mm long, smooth or irregularly furrowed when dry, narrowed at the mouth, red brown; exothecial cells small, red, very thick-walled in 5–7 rows below the mouth, firm-walled, irregularly short-rectangular below; stomata phaneroporic, at very base of capsule; opercula rostrate to obliquely rostrate, red, 1.0–1.5 mm long; annuli rudimentary, cells clinging to the operculum base and capsule mouth after dehiscence; peristome diplolepideous; exostome teeth narrowly triangular, yellowish white, lightly papillose, outer trabeculae lightly thickened, inner trabeculae thick, to 0.3 mm long; endostome basal membranes very low, pale, lightly papillose, segments and cilia absent. Spores finely papillose, round, 20–25 µm, and irregularly oblong, 45–60 µm, endosporically germinated within the capsule, endosporic protonemata 70–110 µm. Calyptrae cucullate, yellowish, smooth, naked, 4–5 mm long.

Illustrations. Hampe (1844, Pl. 16); Bartram (1949, Fig. 110 A–B); Sharp *et al.* (1994, Fig. 500); Churchill and Linares (1995, Fig. 118 d–j). Figure 28.

Habitat. On tree trunks and branches (*Alnus*, *Buddleja*, *Cupressus*, *Erythrina*, *Juniperus*, *Quercus*), logs, rotting wood, rocks, and sandy soil; 1950–3700 m.

Distribution in Central America. GUATEMALA. Huehuetenango: *Standley 84521* (F, FH); Quetzaltenango: *Sharp 2088* (FH, MO, US); Quiché: *Sharp 2541* (FH, MO, US); San Marcos: *Sharp 5455* (FH, MO, US); Totonicapán: *Standley 84521* (F, FH). COSTA RICA. San José: *Crosby & Crosby 5737* (MO). PANAMA. Chiriquí: *Allen 9148* (MO, PMA).

World range: Mexico; Central America; Western and Northern South America.

Leucodon curvirostris is a medium-sized to robust species with plicate, narrowly acuminate leaves that are typically loosely erect at base and secund above. There are some collections (*e.g.*, *Sharp 2541* and *Allen 9148*) with stiffly erect, non-secund leaves, and these have a very different aspect from the typical expression of the species. In size and leaf form these collections are typical of *L. curvirostris*. The sporophytes of *L. curvirostris* are remarkably variable. Its capsules can be subglobose, oval, or oblong-ellipsoid, and seta length varies from 4 to 12 mm. Since the perichaetial leaves of *L. curvirostris* are long and sheathing, the capsules vary from long-exserted to emergent. The degree of capsule exsertion varies not only between but also within collections.

The capsules of *L. curvirostris* contain spores of two sizes. The vast majority of the spores are greatly enlarged (45–60 µm) and irregularly shaped. Scattered among these enlarged spores are a few small (20–25 µm), round spores, and these appear to be viable. The spores of *L. curvirostris* undergo endosporic germination within the capsule and these multicellular structures can be as large as 110 µm. Endosporic germination apparently occurs late in development, and mature capsules with intact opercula contain mostly enlarged spores.

Leucodon cryptotheca Hampe is a Mexican endemic similar to *L. curvirostris* in size and aspect. It has immersed capsules and this feature is often used to distinguish the two species, but, since *L. curvirostris* can have emergent capsules, this distinction needs to be carefully evaluated. In *L. cryptotheca* the capsules are fully immersed, with the perichaetial leaves overtopping the capsules. In contrast, collections of *L. curvirostris* with emergent capsules never have the perichaetial leaves overtopping the capsules. The leaves of *L. cryptotheca* and *L. curvirostris* also have different apices. In

L. cryptotheca they are broadly acuminate, while those of *L. curvirostris* are narrowly acuminate and more sharply pointed. The leaf apex illustrations of these two species in Sharp *et al.* (1994, Figs. 499 B & 500 C) clearly show their differences.

Plants of *Leucodon brachypus* approach those of *L. curvirostris* in size, and both species have plicate, secund leaves. The leaves of *L. brachypus*, however, are smaller than those of *L. curvirostris* and they are generally more tightly erect at base. Furthermore, the leaf apices in *L. brachypus* are broader than those of *L. curvirostris*, with usually shorter apical leaf cells, and its capsules are immersed or laterally emergent.

LEPYRODONTACEAE

Lepyrodontaceae Broth., Nat. Pflanzenfam. I(3): 771. 1906.

Plants in glossy, spreading mats, or deep, dense cushions and tufts, densely matted with reddish brown tomentum. Stems creeping or erect, in cross section with small, thick-walled epidermal cells, cortex cells enlarged, thin-walled, central strand present; rhizoids arising from sparse macronemata around branch buds or from initials in leaf axils. Stem leaves triangular-ovate to lanceolate. Branch leaves smooth or variously plicate, often hair-pointed, auriculate or rounded at base; margins plane, erect, incurved, or recurved, entire, serrulate or serrate; costae single, at times ending at midleaf, often spurred, or short and double, broad and bulging at base; cells long, sigmoid to linear-vermicular, smooth or occasionally prorate above, more or less porose, firm-walled; alar cells shorter, at times with a few subquadrate cells. Asexual reproduction by flagellate branches or by caducous leaves. Dioicous. Male plants full-sized or dwarfed; perigonia lateral. Perichaetia gemmate, lateral on lower sides of stems, often in tomentum. Setae single or multiple, long, smooth; capsules erect to suberect, cylindric, subcylindric to cupulate; stomata superficial or immersed on capsule neck; annuli compound and deciduous; opercula conic at base, obliquely rostrate; peristome diplolepideous, single or double; exostome absent or with 16 short, reduced, hyaline, slightly papillose teeth; endostome reduced, hyaline, slightly papillose or smooth, basal membranes low, segment perforation gaps irregularly developed, cilia absent or present as 1–2 rudimentary stubs. Spores slightly papillose. Calyptrae cucullate, naked.

The Lepyrodontaceae are a monogeneric family, which Fleischer (1908) positioned between the Ptychomniaceae and the Pterobryaceae. Since then the Lepyrodontaceae have continued to be associated with either the Ptychomniaceae (Fleischer 1923; Brotherus 1925; Sainsbury 1955; Scott 1976; Buck & Vitt 1986) or the Pterobryaceae (Crum 1994c; Buck 1998; Buck & Goffinet 2000; Goffinet & Buck 2004).

Evidence for a relationship between the Ptychomniaceae and Lepyrodontaceae is mostly gametophytic. The families are dioicous and they have leaves with short, weak variable costae, linear-vermicular, incrassate and porose leaf cells, weakly differentiated alar cells, and cucullate calyptrae. The families differ in the position of their rhizoids. In the Ptychomniaceae the rhizoids originate from initials clustered on the stem abaxial to the leaf insertions. The rhizoids in the Lepyrodontaceae arise from initials around branch buds or in the leaf axils. The sporophytes of the Ptychomniaceae are considerably different from those of the Lepyrodontaceae. In the Ptychomniaceae the capsules are strongly 8-ribbed, the conic opercula have long, needle-shaped rostra (sometimes as long as the capsule), the exostome teeth are cross-striate, often strongly furrowed, and the exothecial cells are usually collenchymatous. In contrast, the Lepyrodontaceae have smooth capsules, short-rostrate opercula, smooth to papillose exostome teeth, and non-collenchymatous exothecial cells. The Pterobryaceae differ from the Lepyrodontaceae in having a dendroid habit, filamentous pseudoparaphyllia, prostome peristomial development, differentiated alar cells, and a pattern of rhizoid initiation similar to that of the Ptychomniaceae.

1. *Lepyrodon* Hampe, Ann. Sci. Nat., Bot. sér. 5, 4: 367. 1865.

Plants small, medium-sized to robust, in glossy, spreading mats, or deep, dense cushions and tufts, bright green, pale green, or yellow green above, brown below, densely matted with reddish brown tomentum. Stems creeping or erect, in cross section with 2–3 rows of small, thick-walled epidermal cells, cortex of enlarged, hyaline, thin-walled cells, central strand variably developed; axillary hairs 3–6 cells long, 1–2 basal cells small, quadrate, red brown, 1–4 upper cells narrow, elongate, hyaline; rhizoids arising from sparse macronemata around branch buds or from initials in leaf axils. Stem leaves erect to wide-spreading when dry, triangular-ovate to lanceolate. Branch leaves erect when dry, smooth or strongly to moderately plicate, oblong, ovate, elongate-triangular, lanceolate or linear, acute, acuminate, often hair-pointed, auriculate or rounded at base; margins plane to erect or incurved below, plane, erect, recurved, or incurved above, entire, serrulate or serrate; costae single, at times ending at midleaf, often spurred, or short and double, broad and bulging at base, lower cross section

consisting of 2–3 ventral layers of enlarged, thin-walled, hyaline cells and a non-stereid dorsal layer of smaller cells, upper cross section with guide cells and a single ventral layer of enlarged, subhyalocysts smaller than guide cells, stereids present or absent; cells long, sigmoid to linear-vermicular, smooth or occasionally prorate above, more or less porose, firm-walled; alar cells shorter, at times with a few subquadrate cells, otherwise not differentiated. Asexual reproduction by flagellate branches or by caducous leaves; flagellate branch leaves erect to loosely erect, ovate-lanceolate, concave, smooth, often ecostate or with a short double costa. Dioicous. Male plants full-sized or dwarfed with perigonia borne laterally. Perichaetia small, bud-like, lateral on lower sides of stems, in tomentum, leaves sheathing the setae at base. Mono- or plurisetous, setae long, red to reddish brown, smooth; capsules erect to suberect, cylindric, subcylindric to cupulate, variously constricted and furrowed at neck; stomata superficial or immersed, on capsule neck; annuli compound and deciduous; opercula conic at base, obliquely rostrate; peristome diplolepideous, single or double; exostome absent or with 16 short, reduced, hyaline, slightly papillose teeth; endostome reduced, hyaline, slightly papillose or smooth, basal membranes low, segment perforation gaps irregularly developed, cilia absent or 1–2 rudimentary stubs. Spores slightly papillose. Calyptrae cucullate, naked.

Lepyrodon Hampe is a mostly Southern Hemispheric genus of seven species commonly found on the ground, tree trunks, and soil over rocks. It is a pleurocarpous moss characterized by: (1) rhizoids from scattered initials around branch buds or in the leaf axils; (2) variable and weakly developed costa; (3) long, linear, firm-walled leaf cells, alar cells poorly developed; (4) dioicous sexual condition (dwarf male plants common); (5) erect, smooth capsules; (6) obliquely rostrate opercula; (7) reduced diplolepideous peristome (exostome commonly absent); and (8) cucullate calyptrae. The genus was revised by Allen (1999).

The name *Lepyrodon* combines the Greek *lepyron* (scale or membrane) with *odontos* (tooth), and it refers to the peristome, which consists chiefly of an endostome.

Lepyrodon tomentosus (Hook.) Mitt., J. Linn. Soc., Bot. 12: 421. 1869. *Neckera tomentosa* (Hook.) Müll. Hal., Syn. Musc. Frond. 2: 111. 1850. *Leucodon tomentosus* Hook., Musci Exot. 1: 37. 1818. Protologue. [Ecuador] In sylvis Cinchonae prope Loxam, regione temperata, altit. 1080 hexapod. *Humboldt et Bonpland*. Type. In sylvis Cinchonae prope Loxam [Loja], *Humboldt & Bonpland* (BM, holotype).

Isopterygium semicostatum Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 41(1): 143. 1905. Protologue. [Costa Rica] Forêts de General, (*Pittier 5817*). Type. San José: forêts de General, *Tonduz* [*Pittier*] *5817* (US, isotype).

Lepyrodon tomentosus var. *latifolius* E. B. Bartram, Contr. U. S. Natl. Herb. 26: 90. 1928. Protologue. On tree, Cerro de las Vueltas, Province of San José, Costa Rica, altitude 2700 to 3000 meters, *Paul C. Standley* and *Juvenal Valerio*, December 29, 1925 to January 1, 1926, *no. 43841*. Types. Costa Rica. San José: Cerro de las Vueltas, *Standley & Valerio 43841* (US, holotype; FH, NY, isotypes).

Lepyrodon duellii H. A. Crum, Bryologist 87: 207. 1984. Protologue. Mexico. Veracruz, "Am Pass Porto de Aire, c. 10 km vor Acultzingo, Bergnebelwald; Lehme; um 2300 m s.m: Borke bzw. Baumbas.," Aug. 21, 1975, *Düll 248*. Types. Mexico. Veracruz: Pass Porto de Aire, ca. 10 km from Acultzingo, *Düll 248* (TENN, holotype; MICH, isotype).

Plants robust, medium-sized, or small, glossy, in spreading mats or occasionally in deep, dense cushions and tufts, bright green, pale green, or yellow green above, brown below, densely matted with reddish brown tomentum, 1–6 cm high. Stolons creeping, leaves narrowly lanceolate, erect to widespreading when dry; margins plane to erect above and at base, serrate to serrulate throughout. Stems erect, in cross section with 2 rows of small, thick-walled epidermal cells, cortical cells enlarged, hyaline, thin-walled, central strand well developed; axillary hairs fragile, 4–5 cells long, 2 basal cells small, quadrate, red brown, 2–3 upper cells narrow, elongate, hyaline. Branches horizontal or erect; lower leaves tumid-imbricate or loosely erect when dry, erect-tumid when wet, smooth, concave, oblong to broadly ovate, acuminate, gradually or abruptly narrowed to a short or long hair-point, upper leaves erect-imbricate when wet or dry, strongly to moderately (rarely weakly) plicate, linear-lanceolate, (1.7–)3–5(–6) × 0.5–1.0 mm, acuminate, narrowed to a long, capillary hair-point to 1 mm long, not or weakly auriculate at base; costae single at times ending at midleaf and often spurred or short and double, broad and bulging at base, lower cross section of 2–3 ventral layers of enlarged, thin-walled,

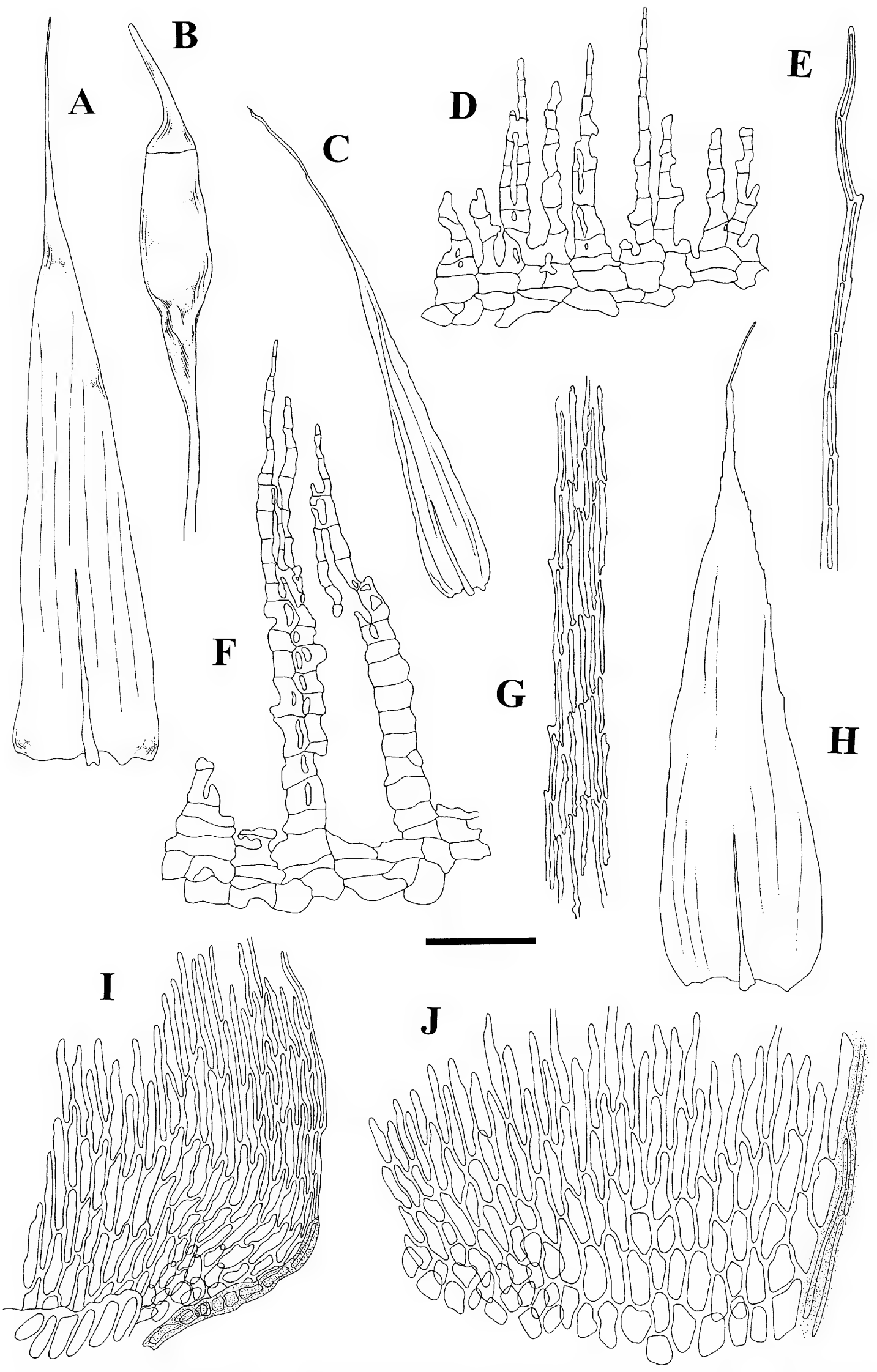
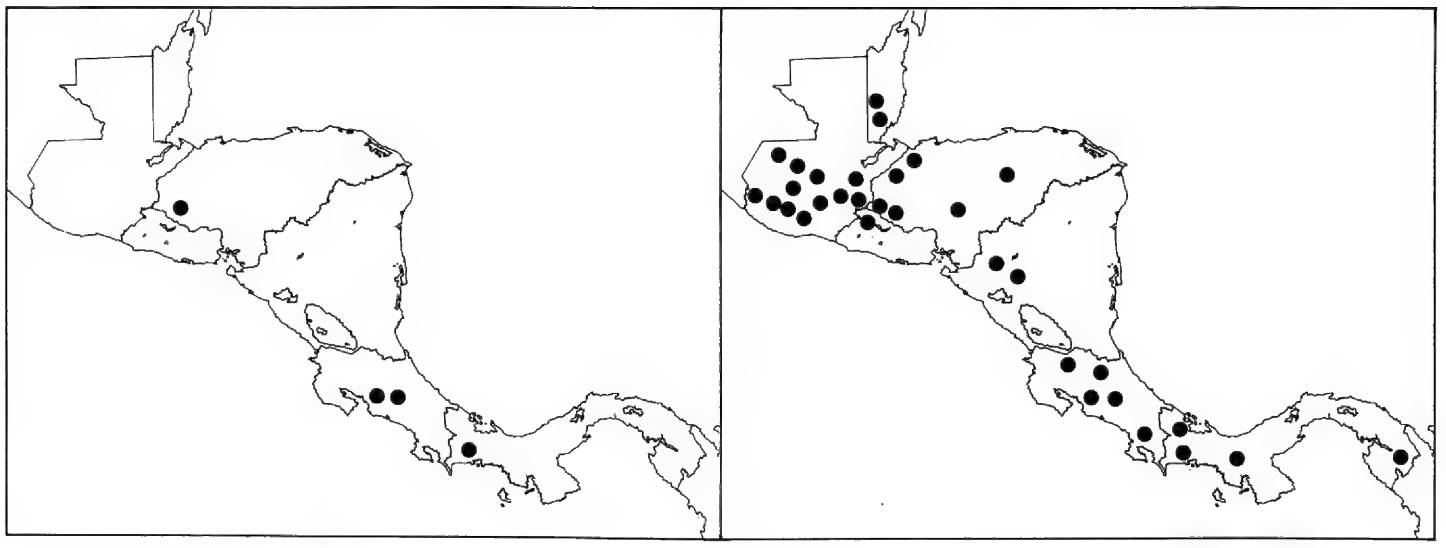


Figure 29. *Lepyrodon tomentosus*. A, C & H. Leaves. B. Capsule. D & F. Endostomes ventral (inner) surfaces. E. Leaf hair-point. G. Leaf margin. I. Leaf alar region. J. Basal leaf cells across the leaf insertion. Scale in mm: bar = 0.06 (E, G, I, J); bar = 0.6 (A, C, H); bar = 0.13 (D, F); bar = 0.29 (B). A, I from *Escobar 1011*; B, F from *Tupayachi & Galiano 1179*; H, J from *Allen 12107*; all other figure parts from *Crosby 11768*.



Lepyrodon tomentosus *Prionodon densus*

hyaline cells and a non-stereid dorsal layer of smaller cells, upper cross section with guide cells and single ventral layer of enlarged, subhyalocyst cells, stereid cells absent; apical cells long-sigmoid to linear-vermicular, smooth, more or less porose, firm-walled, 30–75 × 4–6 µm; basal cells 50–90 µm long; alar cells shorter, otherwise not differentiated. Asexual reproduction by flagellate branches; flagellate branch leaves erect to loosely erect, ovate-lanceolate, concave, smooth, often ecostate or with a very short, double costa. Dioicous. Male plants to 10 mm long, leaves widely spaced, narrowly lanceolate; perichaetia gemmate, lateral on lower sides of stems in tomentum. Setae single, 5–18 mm long. Capsules 2–4 mm long, erect to suberect, cylindric, subcylindric to cupulate; exothecial cells irregularly quadrate to short-rectangular, thick-walled; opercula to 1.5 mm long; peristome single and endostomial; endostome to 700 µm high, hyaline, smooth, basal membranes to 70 µm high, segment perforation gaps irregularly developed, cilia absent or rudimentary. Spores 15–25 µm, papillose. Calyptrae cucullate, naked, to 6 mm long.

Illustrations. Hooker (1818, Pl. 37); Brotherus (1906b, Fig. 580 A–G); Brotherus (1925, Fig. 516 A–G); Bartram (1928a, Fig. 29 A); Crum (1984, Figs. 14–18); Sharp *et al.* (1994, Fig. 523 a–e); Allen (1999, Figs. 20 a–h & 21 a–j). Figure 29.

Habitat. On tree trunks, branches or twigs, rotting logs or stumps, rocks, boulders or fissures of shaded cliffs (granite and slate), in forests or terrestrial; 300–4800 m.

Distribution in Central America. HONDURAS. Lempira: *Allen 12086* (CBG, H, MO, NY, S, TEFH). COSTA RICA. Cartago: *King C-74-56* (MO); San José: *Crosby & Crosby 6121* (CR, MO). PANAMA. Chiriquí: *Allen 9149B* (MO, PMA).

Distribution. Mexico; Central America; Caribbean; Western, Northern, and Southern South America, Brazil.

Lepyrodon tomentosus is remarkably variable in size, stance, and aspect. The species characteristically has plicate, narrowly acuminate upper branch leaves that end in long capillary hair-points, and narrowly elongate upper leaf cells. Interestingly, the lower branch leaves in this species, which are smooth, concave, and oblong to broadly ovate, are identical in form to the leaves of the South American *L. lagurus* (Hook.) Mitt. *Lepyrodon tomentosus* has three distinctive expressions that are more or less geographically restricted and may be worthy of recognition as varieties.

The type expression of *L. tomentosus* is common in the Andes of western South America and is also found in Mexico and northwestern Argentina. It is a robust plant with large (4–6 mm long), stiffly erect, linear-lanceolate, non-auriculate, strongly plicate leaves, moderately developed *lagurus*-type branch leaves, and long setae. The second expression of *L. tomentosus* is typified by *L. tomentosus* var. *latifolius*. It is the most commonly encountered expression of *L. tomentosus*, present from southern Mexico through Ecuador, and in the Dominican Republic as well as southeast Brazil. This expression is moderate in size, with laxly erect, concave, weakly plicate, broadly lanceolate leaves, unusually short and often double costae, and setae that are variable in length. In this expression of the

species the *lagurus*-type branch leaves often occupy more than half the branch length, and sometimes a large majority of leaves are of this form (see, *e.g.*, *Allen 12107*, MO, Honduras). The extreme in this expression is seen in the type of *L. duellii*, a small, depauperate collection that consists almost entirely of *lagurus*-type leaves. In Chile and southwestern Argentina, *L. tomentosus* is represented by an expression that has small plants with stiffly erect, linear, non-auriculate leaves (1.7–3 mm long) that are often twisted and undulate when dry. The leaves in this expression have long, capillary hair-points, and its *lagurus*-type lower branch leaves often approach the form of the stolon leaves. The setae in this expression are always short. This expression is present in the Dominican Republic, but otherwise is restricted to southern South America.

The costa in *L. tomentosus* is broad, thickened at base, and continues down the stems considerably farther than the leaf lamina. Most of the costa in this region consists of multiple layers of greatly enlarged, thin-walled hyaline cells. These cells can be seen on the stems at the base of the leaf insertion lines after the leaves have been removed. Asexual reproduction by means of flagellate branches is common in all forms of *L. tomentosus*.

PRIONODONTACEAE

Prionodontaceae Broth., Nat. Pflanzenfam. I(3): 763. 1905.

Plants robust, in lax tufts. Primary stems creeping; leaves reduced, scale-like; rhizoids red, smooth, branched or unbranched, from circular clusters of initials abaxial to the leaf insertions. Secondary stems erect, simple, irregularly or regularly pinnately branched, at times stipitate; cross section with sclerodermis, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; scale leaves present; rhizoids rarely present on secondary stems. Secondary stem and branch leaves differing primarily in size; leaves ovate-lanceolate, at times plicate, undulate, or rugose, decurrent, apices at times fragile, narrowly acuminate; margins plane, sometimes narrowly recurved below, coarsely serrate above, teeth uni- or multicellular, marginal cells at times obscurely to distinctly differentiated; costae single, subpercurrent, at times wavy above; cells smooth or unipapillose, upper and median cells variable in shape, quadrate, short-rectangular, elliptic-oblong, or fusiform; basal interior cells near costae elongate to linear, porose or non-porose, firm- to thick-walled; alar cells strongly differentiated. Dioicous. Perigonia and perichaetia lateral, gemmate; paraphyses present. Setae short or long, smooth or scabrous. Capsules emergent to long-exserted, globose to oval, ovate or subcylindrical; stomata on capsule neck; opercula rostrate; annuli simple or complex and deciduous; peristome diplolepideous, yellowish white; exostome teeth linear, papillose; endostome absent or reduced, basal membranes low, segments linear, flat, united at the tips, cilia absent. Spores round, papillose. Calyptrae cucullate, naked.

The Prionodontaceae were originally established as a monogeneric family (Brotherus 1905b). The family was expanded to include *Neolindbergia* M. Fleisch. (Fleischer 1908) and *Taiwaniobryum* Nog. (Noguchi 1936). *Neolindbergia* is similar to the Pterobryaceae in its habit, overall aspect, and peristome morphology. Akiyama *et al.* (1991) were the first to note the presence of filamentous pseudoparaphyllia in *Neolindbergia*, and this seems to indicate the genus is best placed in the Pterobryaceae (see Crosby & Magill 1977, 1981; Akiyama *et al.* 1991; Buck 1998; Buck & Goffinet 2000; Goffinet & Buck 2004). The positioning of *Taiwaniobryum* is more problematical. Buck (1998) tentatively placed *Taiwaniobryum* in the Leptodontaceae. However, *Taiwaniobryum* is similar to *Prionodon* in habit, stem cross section morphology, branching pattern, leaf form and marginal dentation, cellular areolation, capsule shape, and the tendency for its marginal leaf cells to be obscurely differentiated. It differs from *Prionodon* in having smooth leaf cells, long, scabrous setae, and no endostome (Noguchi 1936, 1989; Lai & Koponen 1981). The endostome in *Prionodon* is a highly distinctive feature of the genus, because its segments are united at the tips forming a trellis-like structure. Nevertheless, since *Taiwaniobryum* lacks endostomial segments, the feature is not useful in evaluating its familiar relationships. On balance, after considering all its features, *Taiwaniobryum* appears properly placed in the Prionodontaceae.

The Prionodontaceae have creeping stolons with reduced leaves and erect, often stipitate, secondary stems that lack paraphyllia and internal differentiation. Their rhizoids are not or weakly branched and generally come from circular clusters of initials at the abaxial side of the stolon leaf insertions. The leaves have strong single costae. The leaf cells are thick-walled, often porose, papillose or smooth, and the basal cells in the alar region are often quadrate to oblate. The family is dioicous, perichaetial leaves are weakly differentiated, capsules are immersed, emergent or long-exserted, and its peristomes are whitish yellow and reduced. The calyptrae are cucullate.

1. *Prionodon* Müll. Hal., Bot. Zeitung (Berlin) 2: 129. 1844.

Plants robust, in lax tufts. Primary stems creeping; leaves reduced, scale-like; rhizoids red, smooth, branched or unbranched, from circular clusters of initials abaxial to the leaf insertions. Secondary stems erect, simple, irregularly or regularly pinnately branched, at times stipitate; cross section with sclerodermis, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; scale leaves present; rhizoids rarely present on secondary stems. Secondary stem and branch leaves differing only in size; leaves ovate-lanceolate to narrowly lanceolate from an ovate base, plicate, decurrent, leaf apices fragile, often detached, narrowly acuminate; mar-

gins plane, sometimes narrowly recurved below, coarsely serrate above, teeth uni- or multicellular, marginal cells at times obscurely to distinctly differentiated; costae single, subpercurrent, at times wavy above, in cross section at base with two rows of guide cells, dorsal and ventral stereid cells; cells unipapillose, upper and median cells variable in shape, quadrate, short-rectangular, elliptic oblong, or fusiform, porose or non-porose, marginal cells often longer and thinner forming a more or less distinct border; basal cells near costae elongate, porose; alar cells strongly differentiated. Dioicous. Perigonia and perichaetia lateral, gemmate. Setae short, red. Capsules emergent to short-exserted, globose to oval or ovate to subcylindrical; exothecial cells short-rectangular to subquadrate, firm-walled; stomata phaneroporic, on capsule neck; opercula rostrate; annuli complex, deciduous; peristome diplolepideous, yellowish white; exostome teeth linear, smooth to weakly papillose at very base, densely papillose above; endostome reduced, smooth to weakly papillose at very base, densely papillose above, basal membranes low, segments linear, not keeled, with strong lateral projections, united at the tips, cilia absent. Spores round, papillose. Calyptrae cucullate, smooth, naked.

Prionodon, a genus of four species, is found only in the Neotropics and Africa (including Madagascar and the Mascarene Islands). Although predominantly corticolous, the genus occasionally occurs on rocks. Plants of *Prionodon* are robust; they have distinct stolons appressed to the substrate and (at times stipitate) simple or variously branched secondary stems at more or less right angles to the stolons. Especially robust plants on tree trunks can have festooning habit. Rhizoids are more or less restricted to the stolons, but sometimes also occur at the base of the secondary stems. The genus has strongly toothed leaves with single, long, at times wavy, costae, and unipapillose, firm-walled, often porose leaf cells. Its leaf cells are variable in shape, but typically those in the basal median region are elongate, and its alar cells are strongly differentiated. *Prionodon* is a dioicous genus and capsules are rarely encountered. It has smooth, cucullate calyptrae, a well-developed, deciduous annulus, and reduced peristomes that consist of whitish yellow, linear, papillose exostome teeth and an endostome with a short basal membrane, no cilia, and flat, linear segments that are united at the tips in the same manner as those of *Fontinalis* Hedw.

The name *Prionodon* combines the Greek *prion* (a saw) with *odontos* (tooth) and refers to the long, broad serrations on margins of its linear endostome segments. These serrations correspond to the lateral extensions on the segments that unite them at the apex into a trellis-like structure.

1. Alar cells nearly all elongate . . . . . 2. *P. fuscolutescens*
1. Alar cells variably quadrate or oblate 2

2. Alar cells restricted to a more or less spherical basal region . . . . . 3. *P. luteovirens*
2. Alar cells in a V-shaped pattern extending along the margins to or nearly to the widest part of the leaf . . . . . 1. *P. densus*

1. *Prionodon densus* (Hedw.) Müll. Hal., Bot. Zeitung (Berlin) 2: 130. 1844. *Hypnum densum* Hedw., Sp. Musc. Frond. 282. 1801. *Pterogonium densum* (Hedw.) Schwägr., Sp. Musc. Frond., Suppl. 3(1): 243. 1828. *Neckera densa* (Hedw.) Wilson, London J. Bot. 6: 292. 1847. *Pilotrichum densum* (Hedw.) Müll. Hal., Syn. Musc. Frond. 2: 160. 1850. Protologue. Jamaica. *Swartz.*

Prionodon dichotomus Hampe, Linnaea 32: 150. 1863. Protologue. [Colombia] In sylv. Tequendama Canoas ad truncos, 2500 metr., Junio, *Lindig 2093*.

Prionodon undulatus Mitt., J. Linn. Soc., Bot. 12: 420. 1869. Protologue. [Colombia and Ecuador] Andes Bogotenses, ad viam inter Tipaquira et Pacho (6000 ped.), ad truncos arborum, *Weir, n. 254*; Paramo do Ruiz, *Purdie.* Andes Quitenses, Quito, *Jameson*, in monte Tunguragua, ad arbores et in monte Guayrapata (9000 ped.), *Spruce, n. 1301*. Types. Andes Bogotenses. Inter Tipaquira et Pacho. alt. 6000. *J. Weir no. 254* (US, syntype); Andes Bogotenses, ad viam inter Tipaquira et Pacho, ad truncos arborum, Alt 6000′, *J. Weir No. 254* (MO, syntype).

Prionodon caldensis Broth., Bih., Kongl. Svenska Vetensk.-Akad. Handl. 21 Afd. 3(3): 44. 1895. Protologue. [Brazil] Prov. Minas Geraës, Caldas, Pedra branca, ad truncos arborum (*Mosén 390*). Type. Brazil. Prov. Minas Geraes, Caldas, Pedra branca, ad truncos arborum *Hj. Mosén 390*, 18 20/8 75 (FH, isotype).

Prionodon nitidulans Broth., Hedwigia 45: 276. 1906. Protologue. [Peru] Rio Huallaga, Cerro de Escalero, 1100 m, an Baumstämmen ([Ule] *n.* 2369). Type. Peru, Departmento Loreto, Baumstämmen, Serra de Escalero 1100 m, *E. Ule 2369* (FH, isotype).

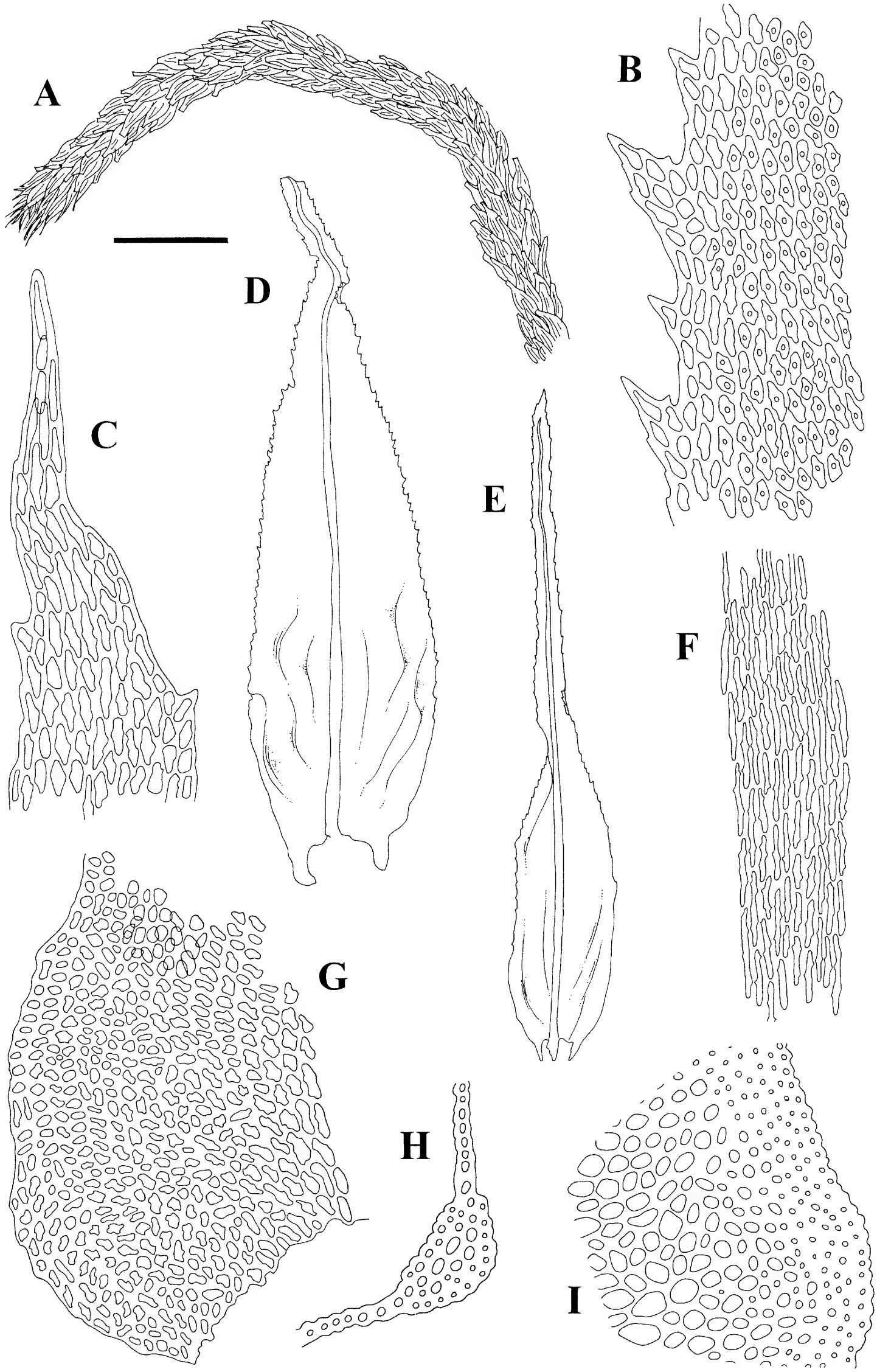


Figure 30. *Prionodon densus*. A. Habit. B. Upper leaf margin. C. Leaf apex. D & E. Leaves. F. Lower leaf cells. G. Leaf alar region. H. Costa in cross section. I. Stem in cross section. Scale in mm: bar = 0.05 (H); bar = 0.06 (B, C, F, G, I); bar = 0.9 (D, E); bar = 6.4 (A). E from *Crosby & Crosby 6225*; all other figure parts from *Allen 14400*.

Prionodon contortus Herzog, Biblioth. Bot. 87: 110. 1916. Protologue. [Bolivia] An Bäumen in der Cordillere von Santa Cruz, ca. 1400 m, [*Herzog*] *No.* 3567; im Bergwald von Florida de San Mateo, ca. 2000 m, [*Herzog*] *No.3702*; im Nebelwald über Comarapa, ca. 2600 m, [*Herzog*] *No. 4278* (f. major). Type. An Waldbäumen in der Kord. von Sta. Cruz, ca. 1400 m, Februar 1911, leg. *Th. Herzog 3567* (FH, syntype), *syn. nov.*

Prionodon mexicanus Thér., Smithsonian Misc. Collect. 78(2): 24. 1926. Protologue. Mexico. Jalapa ([*Arsène*] *8000*); Cerro Azul ([*Arsène*] *4980*); Campanario ([*Arsène*] *7569*). Type. Mexico. Jalapa, Veracruz, 1400 m, *No. 8000 Bro. G. Arsène*, Collector, XII, 1907 (US, syntype).

Prionodon arsenei Thér., Smithsonian Misc. Collect. 78(2): 25. 1926. Protologue. [Mexico] Esperanza ([*Arsène*] *4747*). Type. Mexico. Esperanza, 2400 m. Vicinity of Puebla, State of Puebla, *No. 4747 Bro. G. Arsène*, Collector (US, holotype).

Prionodon densus var. *crispatulus* E. B. Bartram, Contr. U.S. Natl. Herb. 26: 92. 1928. Protologue. On tree between Aserri and Tarbaca, Province of San José, Costa Rica, altitude 1600 to 1900 meters, *Paul C. Standley*, February 12, 1924, *no. 34171*. Types. Costa Rica. On tree. Between Aserrí and Tarbaca, Province of San José; altitude 1600 to 1900 meters, *No. 34171 Paul C. Standley*, Collector, February 12, 1924 (US, holotype; FH, isotype).

Plants robust, in green, yellow green, or yellow brown, lax tufts. Primary stems creeping; leaves reduced, scale-like; rhizoids red, smooth, not or weakly branched, from circular clusters of initials abaxial to the leaf insertions. Secondary stems erect, simple, irregularly or regularly pinnately branched, at times stipitate, 5–17 cm long; cross section with sclerodermis of 3–7 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent, scale leaves present; rhizoids not or only rarely present. Secondary stem and branch leaves differing only in size; leaves ovate-lanceolate, plicate, 4–8 mm long, erect at base, erect to spreading, flexuose to contorted when dry, wide-spreading when wet, decurrent, leaf apices fragile, often detached, narrowly acuminate; margins plane, sometimes narrowly recurved below, coarsely serrate above, teeth uni- or multicellular, marginal cells at times obscurely to distinctly differentiated; costae single, subpercurrent, at times wavy above, in cross section at base with two rows of guide cells, dorsal and ventral stereid cells in multiple rows; cells unipapillose, upper and median cells extremely variable in shape, quadrate, short-rectangular, elliptic-oblong, or fusiform, porose or non-porose, (20–)12–7 × 5–7 µm, marginal cells often longer and thinner forming a more or less distinct border; basal cells near costa elongate, to 60 µm long, porose; alar cells quadrate to oblate, thick-walled, extending in a broad or narrow V-shaped band along the margin to near the widest part of the leaf, occasionally with a few scattered quadrate to oblate cells, 12–30 × 4–6 µm. Dioicous. Perigonia and perichaetia lateral, gemmate, 1–1.5 mm long. Setae 1–1.5 mm long, red. Capsules emergent to short-exserted, globose, oval, ovoid or subcylindrical, 2.0–2.5 mm long, smooth when dry, narrowed at the mouth, red brown; exothecial cells, small, red, very thick-walled in 3–5 rows below the mouth, firm-walled, irregularly short-rectangular below; stomata, operculum, annulus, peristome not seen. Spores round, papillose, 12–18 µm. Calyptrae cucullate, smooth and naked.

Illustrations. Thériot (1926, Figs. 13 & 14); Bartram (1928a, Fig. 29 B–E); Bartram (1949, Fig. 111 D–G); Griffin (1970, Fig. 1 c, e–h); Sharp *et al.* (1994, Fig. 521); Churchill and Linares (1995, Fig. 164 a–c); Duarte Bello (1997, Pl. 178 a–c); Buck (1998, Pl. 70); Magill and Rooy (1998, Fig. 155). Figure 30.

Habitat. On tree (palm, *Cupressus*, *Persea*) trunks, branches, and twigs in canopy, at times forming festoons, also on rotting logs, terrestrial, on boulders, and occasionally on concrete bridges; 750–3500 m.

Distribution in Central America. BELIZE. Cayo: *Allen 15070* (MO); Toledo: *Allen 15366* (MO). GUATEMALA. Baja Verapaz: *Sharp 2913* (MO); Chimaltenango: *Sharp 2583* (MO, US); Chiquimula: *Steyermark* 30820 (FH, US); Guatemala: *Standley 80731* (FH, NY, US); Huehuetenango: *Sharp 4956* (MO, US); Jalapa: *Steyermark 32620* (FH); Quetzaltenango: *Sharp 2277* (MO, US); Quiché: *Sharp 2493* (MO, US); Sacatepéquez: *Standley 65090a* (FH); San Marcos: *Steyermark 36766* (FH); Sololá: *Steyermark 47566* (FH, MO, NY, US); Zacapa: *Steyermark 43309* (FH, US). EL SALVADOR. Chalatenango: *Sipman et al. 37630* (NY); Santa Ana: *Davidse et al. 37212* (MO). HONDURAS. Cortés: *Allen 14400* (MO); Francisco Morázan: *Morton 7387* (US); Lempira: *Allen*

11441 (MO); Ocotepeque: *Allen 14477* (MO); Olancho: *Allen 12798* (MO); Santa Bárbara: *Allen 11657* (MO). NICARAGUA. Estelí: *Grijalva & Araquistain 680* (MO); Matagalpa: *Richards et al. 3744* (MO). COSTA RICA. Alajuela: *Crosby & Crosby 6286* (FLAS, MO); Cartago: *Croat 35422* (BM, CR, DUKE, F, FH, FLAS, MEXU, MO, NY, US); Heredia: *Crosby 10863* (BM, CR, DUKE, F, FH, H, MICH, MO, MEXU, NY, US); Puntarenas: *Crosby 2514* (FLAS, MO); San José: *Griffin & Morales B116* (MO, NY). PANAMA. Bocas del Toro: *Davidse et al. 25341* (MO); Chiriquí: *Allen 5391* (MO, PMA); Darién: *Allen 8862* (MO); Veraguas: *Crosby 10252* (FLAS, MO).

World range: Mexico; Central America; Caribbean; Western and Northern South America, Brazil; Southern Africa; Western Indian Ocean.

Prionodon densus is a common species at higher elevations in Central America, usually found pendent from tree trunks and branches. It has fragile leaves that are often broken above, and is remarkably variable in many of its features. It can be distinguished from other Central American species of *Prionodon* by its well-developed, thick-walled, quadrate to oblate alar cells that extend well up the margins in a V-shaped pattern. There are two distinct forms of *P. densus* in Central America. The most common form has robust plants with unbranched or sparsely branched stems and closely spaced leaves that have exceptionally well-developed alar cells. The other form of *P. densus* consists of more slender plants that are usually subpinnately branched and have well-spaced leaves in which the stems can often be seen with a hand lens. This second form also has more weakly developed alar cells than the common form of the species.

Typically, the alar cells in the common form reach the widest part of the leaf base, and these plants are easy to recognize as *P. densus*. In the second form the alar cells only approach the widest part of the leaf, and these plants are often confused with *P. luteovirens*. Regardless of whether or not the alar cells reach the widest part of the leaf, in both forms of *P. densus* the alar cells are identical in forming a long band of cells along the leaf margins in a manner similar to the alar cells of *Pylaisia selwynii* Kindb.

Prionodon luteovirens and the second form of *P. densus* have slender plants that are commonly pinnately to subpinnately branched and similarly shaped alar cells. In recognizing the slender form of *P. densus*, it is important to observe not only how far the alar cells extend along the leaf margins, but also the overall shape of the alar region. In *P. luteovirens* the alar cells are restricted to the lower part of the leaf base, where they form a more or less circular group of cells. In addition, plants of *P. luteovirens* more often have intact leaves.

Leaf cell form in *P. densus* is remarkably variable from collection to collection. At times the upper and median leaf cells can be quadrate, short-rectangular, or fusiform, and the cells can be strongly porose or non-porose. Furthermore, the upper marginal leaf cells are often elongate forming a more or less distinct border. Basal leaf cell form is also variable, with the cells varying from short-rectangular to elongate-linear. The basal leaf cells, however, are consistently porose. *Prionodon densus* exhibits such remarkable variation in leaf cell form that it is difficult to accept it as a single taxon, without the benefit of examining a large series of collections. The marginal teeth on the leaves of *P. densus* vary from sharply serrate to broadly dentate and can consist of single or multiple cells.

Robinson (1967) applied the name *Prionodon dichotomus* to what is here recognized as *P. luteovirens*. Griffin (1973) attributed this problem to confusion over the type specimen of *P. dichotomus*, and he emended the original description of the species to include "dense alar cells extending along the basal margin to widest part of the leaf." *Prionodon densus* differs from *P. dichotomus* only in having globose to oval rather than ovoid to subcylindrical capsules. In a genus that rarely has sporophytes this distinction is impractical, and in the absence of any other distinguishing features they are here considered synonyms.

2. *Prionodon fuscolutescens* Hampe, Ann. Sci. Nat., Bot., sér. 5, 4: 357. 1865. Protologue. [Colombia] Bogota, Pacho, 2200 m, in sylv. Julio 1863 leg. *A. Lindig*.

Plants robust, in green, yellow green, or reddish yellow, lax tufts. Primary stems creeping; leaves reduced, scale-like; rhizoids red, smooth, not or weakly branched, from circular clusters of initials abaxial to the leaf insertions. Secondary stems erect, simple or irregularly branched, 8–20 cm long;

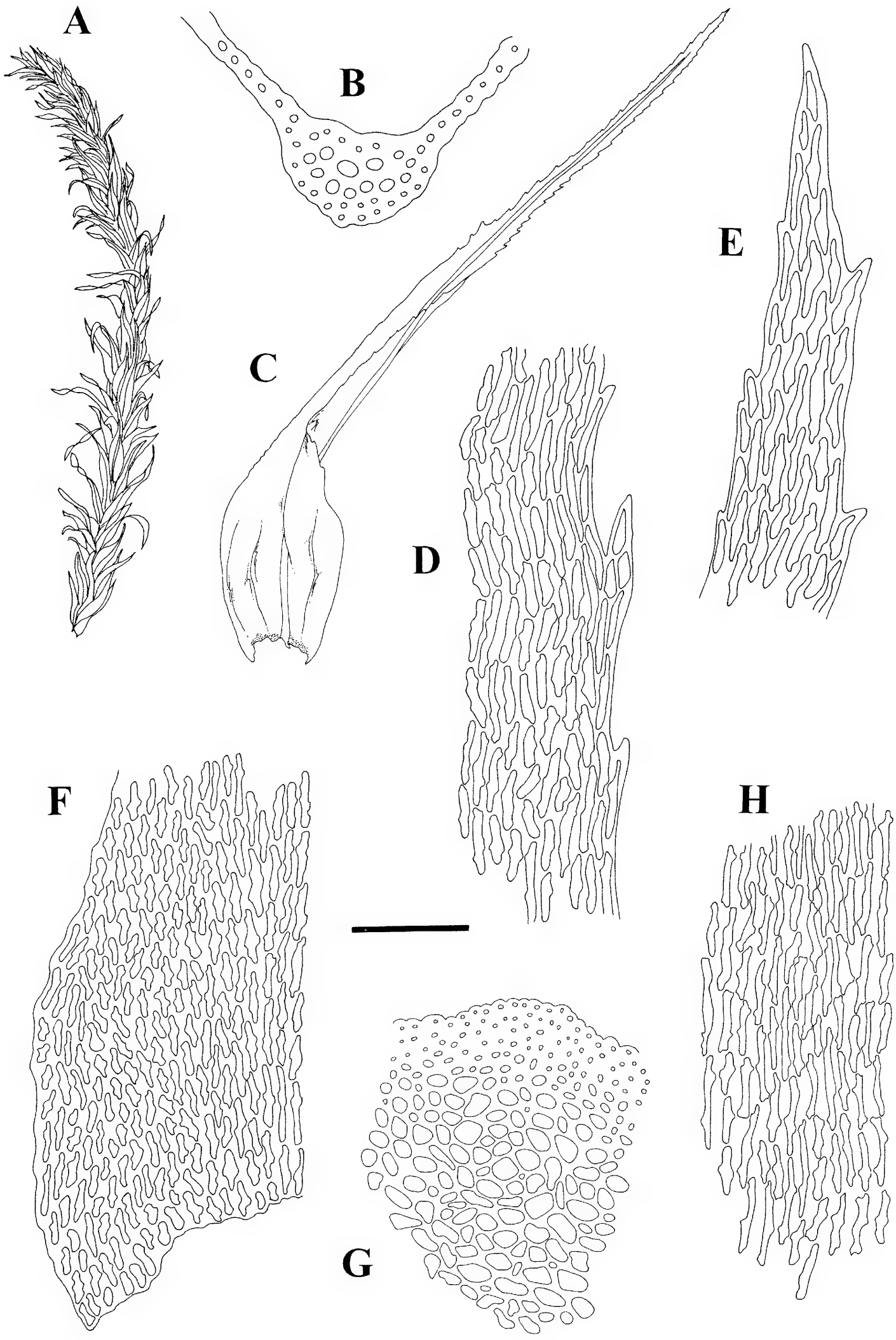
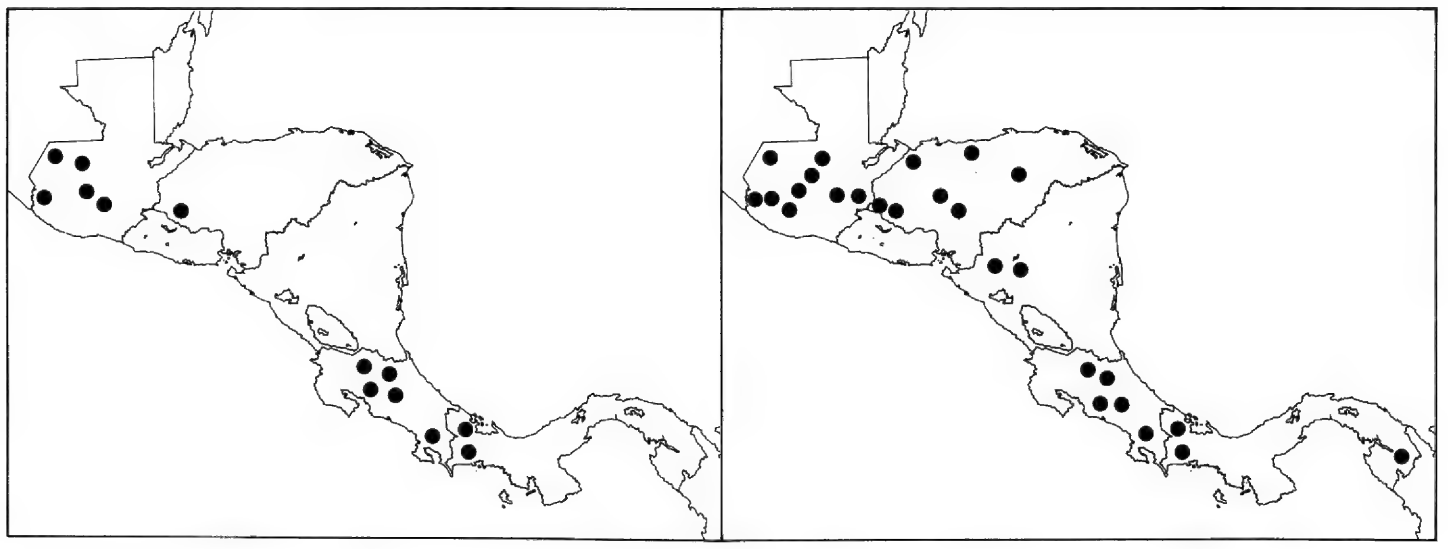


Figure 31. *Prionodon fuscolutescens*. A. Habit. B. Costa in cross section. C. Leaf. D. Marginal leaf cells at mid-leaf. E. Leaf apex. F. Basal leaf cells. G. Stem in cross section. H. Median leaf cells. Scale in mm: bar = 0.05 (B); bar = 0.06 (D–F, H); bar = 0.08 (G); bar = 1.25 (C); bar = 5.1 (A). B & G from *Crosby 9852*; all other figure parts from *Allen 5278*.



Prionodon fuscolutescens *Prionodon luteovirens*

cross section with sclerodermis of 3–5 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent, scale leaves present; rhizoids not or only rarely present. Secondary stem and branch leaves differing only in size, leaves long, narrowly lanceolate from an ovate base, plicate, apices fragile, often detached, 7–10(–12) mm long, erect at base, erect to wide-spreading above when dry, wide-spreading to subsquarrose when wet, decurrent, narrowly acute to acuminate; margins plane, sometimes narrowly recurved below, coarsely serrate above, teeth uni- or multicellular; costae single, subpercurrent, at times wavy above, in cross section at base with two rows of guide cells, dorsal and ventral stereid cells in multiple rows; cells unipapillose, typically elongate and porose throughout, at times upper cells fusiform, 20–60 × 4–8 µm; alar cells usually elongate and porose, occasionally with a few scattered quadrate to oblate cells, 12–30 × 4–6 µm. Dioicous. Sporophytes not seen; "Setae 2–3 mm long; capsules ovoid, 2–3 mm long" (Griffin 1994).

Illustrations. Bartram (1949, Fig. 111 A–C); Sharp *et al.* (1994, Fig. 519); Churchill and Linares (1995, Fig. 164 d–h). Figure 31.

Habitat. On tree trunks and branches in cloud forests and bogs, at times pendent, also terrestrial on road banks; 1250–3333 m.

Distribution in Central America. GUATEMALA. Chimaltenango: *Standley 57826* (FH); Guatemala: *Standley 80723* (FH, NY); Huehuetenango: *Steyermark 48484* (FH, MO, US); Quiché: *Sharp 2493* (FH); San Marcos: *Standley 86439* (FH, NY). HONDURAS. Lempira: *Allen 12123* (MO). COSTA RICA. Alajuela: *Standley & Torres 47765* (FH, US); Cartago: *Crosby & Crosby 6360* (CR, FLAS, MO); Heredia: *Crosby 13149* (MO); Puntarenas: *Lyon 333* (MO); San José: *Crosby & Crosby 6239* (CR, FLAS, MO). PANAMA. Bocas del Toro: *Allen 5278* (MO); Chiriquí: *Croat 48621* (MO, US).

World range: Mexico; Central America; Western and Northern South America.

Prionodon fuscolutescens is a robust species with very long, narrowly acuminate leaves that are subsquarrose when wet. Although its leaves are quite fragile and intact leaves are very hard to find on most stems and branches, those near the apical buds are usually intact. Microscopically, *P. fuscolutescens* is distinguished from the other Central American species of *Prionodon* by its elongate alar cells. In *P. densus* and *P. luteovirens* the leaves have large areas of quadrate to oblate cells in the alar region. Unfortunately, there are occasional collections of *P. fuscolutescens* that have a mixture of elongate and quadrate to oblate alar cells (see, *e.g.*, *Standley 61111*, FH, Guatemala or *Allen 11439, 11554*, MO, Honduras), and these can be difficult to distinguish from *P. densus* or *P. luteovirens*. This expression of *P. fuscolutescens* also has robust, unbranched plants with long, linear, strongly porose basal cells and fairly long upper leaf cells. This is the first report of *P. fuscolutescens* from Mexico. The species was collected in the State of Chiapas (*Breedlove 25840*, MO).

3. *Prionodon luteovirens* (Taylor) Mitt., J. Linn. Soc., Bot. 12: 417. 1869. *Neckera luteovirens* Taylor, London J. Bot. 5: 59. 1846. *Prionodon densus* (Hedw.) Müll. Hal. var. *luteovirens* (Taylor) E. B. Bartram, Fieldiana, Bot. 25: 247. 1949. Protologue. [Ecuador] On Pichincha, near Quito, *Prof. William Jameson*, 1845.

Prionodon laeviusculus Mitt., J. Linn. Soc., Bot. 12: 419. 1869. Protologue. [Colombia] Andes Bogotenses, in sylvis supra Pacho (6000–7000 ped.), copiosus in truncis arborum, *Weir, n. 126*; inter Tipaquira et Pacho (6000 ped.), *Weir, n. 255*, inter Pacho et Turmal (6000 ped.), *Weir, n. 282*; etiam inter muscos, *Funck et Schlim*. Type. Musci Novae-Granatenses, Andes Bogotenses. Supra Pacho, alt. 6000–7000′, *J. Weir No. 126* (US, syntype).

Prionodon longissimus Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32(1): 178. 1894. Protologue. [Costa Rica] Forêts du Barba, versant pacifique, vers 2500 m. (*Pitt*[*ier*] *n*^{o} *5609*, ster.); forêts de l'Irazu (*Pitt*[*ier*] *n*^{o} *5614*, fert.). Types. Costa Rica. Forêts du Barba versant pacifique vers 2500 m, legit *H. Pittier & Tonduz 5609*, 6-2-1890 (FH, US, syntypes).

Prionodon jamesonii Müll. Hal., Hedwigia 40: 56. 1901. Protologue. Ecuador, Quito: *Jameson*, illegitimate name, nomenclaturally superfluous.

Prionodon solorzanoi Cardot, Rev. Bryol. 37: 7. 1910. Protologue. [Mexico] État de Michoacan: San Miguel del Monte, Morelia, 1908, (*D*^{r} *Manuel Martinez Solorzano, no. 8*; D^{r} Pringle comm.). État de Puebla: Honey-station, 1908 (*Pringle, n. 10489*). Types. Plantae Mexicane. State of Hidalgo. On cliffs under a waterfall near Honey Station, 17 June 1908, *C.G. Pringle 10489* (MO, US, syntypes).

Plants robust, in green, yellow green, occasionally reddish yellow, lax tufts. Primary stems creeping; leaves reduced, scale-like; rhizoids red, smooth to lightly roughened, irregularly branched, from circular clusters of initials abaxial to the leaf insertions. Secondary stems erect, dendroid, often regularly pinnately branched, also simple or irregularly branched, 8–50 cm long; cross section with sclerodermis of 3–6 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent, scale leaves present; rhizoids present at base of secondary stems. Secondary stem and branch leaves differing primarily in size, leaves long, narrowly lanceolate from an ovate base, plicate, apices intact or fragile, 3–6 mm long, erect to wide-spreading when dry, wide-spreading to subsquarrose when wet, decurrent, acuminate; margins plane, sometimes narrowly recurved below, coarsely serrate above, teeth uni- or multicellular, marginal cells at times obscurely to distinctly differentiated; costae single, percurrent to subpercurrent, at times wavy above, in cross section at base with two rows of guide cells, dorsal and ventral stereid cells in multiple rows; cells unipapillose, upper cells rhombic to elliptic, porose, 10–20 × 4–6 µm; basal cells near costa fusiform to linear, porose, 20–60 × 4–8 µm; alar cells confined to the basal angles, quadrate to oblate. Dioicous. Perichaetia and perigonia gemmate, lateral along the secondary stems; inner perichaetial leaves aristate. Setae short, 1.0–1.5 mm long, red, smooth. Capsules shortly exserted, ovoid, red, 2–3 mm long; exothecial cells short-rectangular to subquadrate, firm-walled; stomata phaneroporic, on capsule neck; opercula rostrate, 1 mm long; annuli complex, deciduous; peristome diplolepideous, yellowish white; exostome teeth linear, smooth to weakly papillose at very base, densely papillose above; endostome reduced, smooth to weakly papillose at very base, densely papillose above, 0.8 mm long, basal membranes low, segments linear, not keeled, united at the tips, cilia absent. Spores lightly papillose, 14–20 µm. Calyptrae cucullate, smooth, naked, 2.5–3 mm long.

Illustrations. Sharp *et al.* (1994, Fig. 520). Figure 32.

Habitat. On tree trunks and branches, shrubs, bamboo, logs, fence posts, and vines, also pendent from rocks and on wet banks; 1200–3300 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: *Standley 90766* (FH, NY); Baja Verapaz: *Sharp 5194* (US); Chimaltenango: *Standley 60958* (FH); Chiquimula: *Steyermark 30819* (FH, NY); Huehuetenango: *Steyermark 50656* (FH, NY); Jalapa: *Steyermark 32620* (FH, NY); Quetzaltenango: *Standley 85705* (FH, NY); San Marcos: *Steyermark 35865* (FH); Sololá: *Steyermark 47520* (FH, MO, NY, US). EL SALVADOR. Chalatenango: *Sipman et al. 37636* (NY). HONDURAS. Atlántida: *Allen 17492* (MO, TEFH); Comayagua: *Allen 13970* (MO); Cortés: *Allen 14377* (MO); Lempira: *Allen 12074* (MO); Francisco Morazán: *Morton 7188* (FH, US); Ocotepeque: *Allen 14440* (MO); Olancho: *Allen 12681* (MO). NICARAGUA. Estelí: *Stevens 16297* (HNMN, MO, NY, US); Matagalpa: *Granzow de la Cerda & Moreno GC-1528* (DUKE, MO). COSTA RICA. Alajuela:

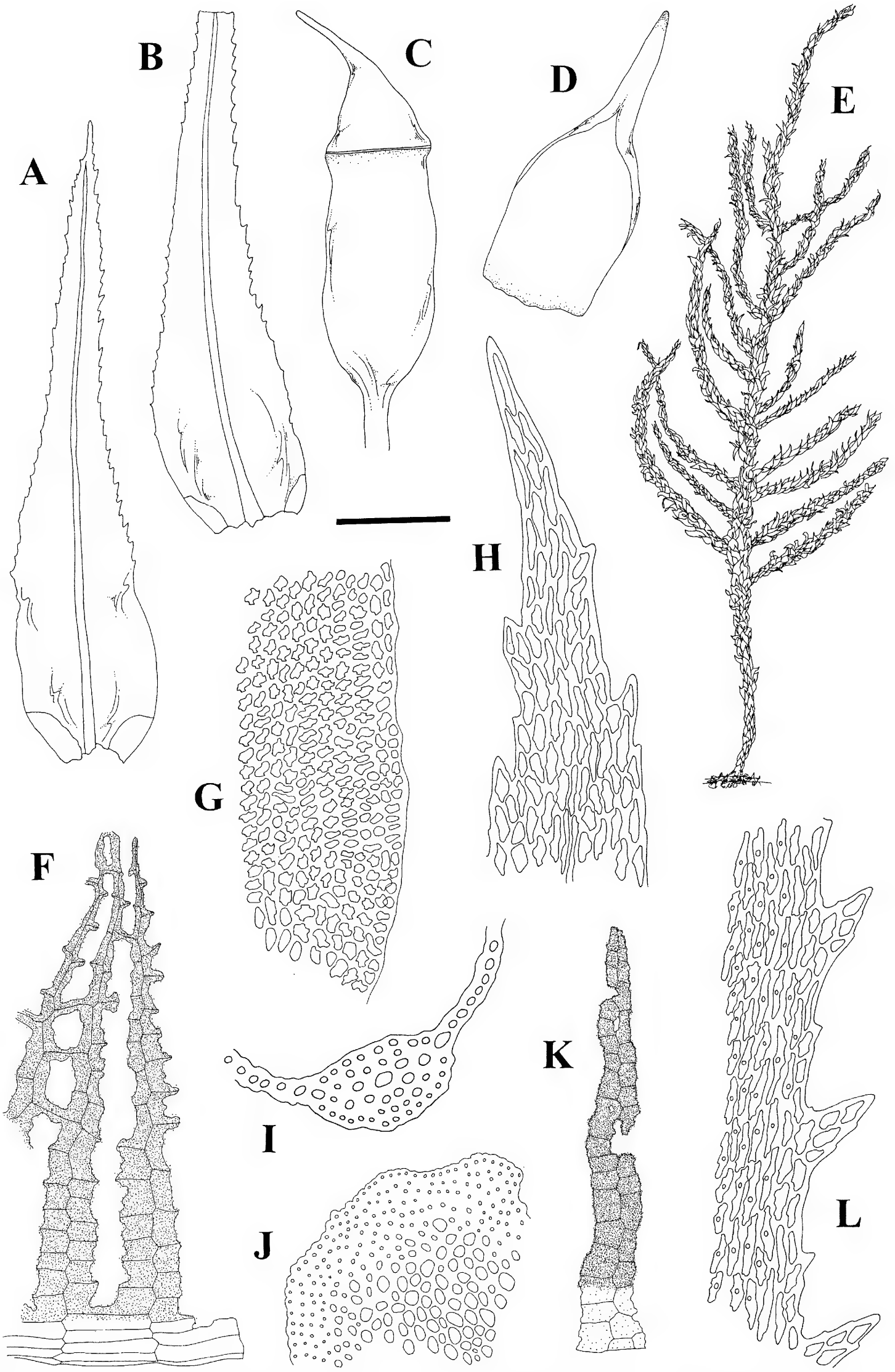


Figure 32. *Prionodon luteovirens*. A & B. Leaves. C. Seta, capsule, and operculum. D. Calyptra. E. Habit. F. Endostome segments, dorsal (outer) surface. G. Basal leaf cells. H. Leaf apex. I. Costa in cross section. J. Stem in cross section. K. Exostome, dorsal (outer) surface. L. Marginal leaf cells at midleaf. Scale in mm: bar = 0.05 (I); bar = 0.06 (G, H, L); bar = 0.08 (J); bar = 0.17 (F, K); bar = 0.6 (A, B, D); bar = 0.9 (C); bar = 5 (E). C, D, F, J, K from *Morton 7188*; all other figure parts from *Allen 14377*.

Crosby & Crosby 6294 (FLAS, MO); Cartago: *Crosby & Crosby 6314* (MO); Heredia: *Crosby 10867* (CR, FH, MO, NY); Puntarenas: *Crosby 2664* (MO); San José: *Standley & Valerio 43543* (FH, US). PANAMA. Bocas del Toro: *Gómez et al. 22489* (MO); Chiriquí: *Croat 34897* (DUKE, H, MEXU, MO, NY, PMA, F, FH, US); Darién: *Mori & Gentry 4370* (FLAS, MO).

World range: Mexico; Central America; Caribbean; Northern and Western South America, Brazil.

Prionodon luteovirens is fairly common in Central America, and it is the only species for which sporophytes have been observed in the region. In its typical expression, *P. luteovirens* has a soft aspect, pinnately branched stems, and intact leaf apices. The soft aspect of the plants is due to its relatively narrow leaves that are well spaced along the stems and branches. The alar cells of *P. luteovirens* are quadrate to oblate and in form closely resemble those of *P. densus*. In *P. luteovirens*, however, they are confined to a more or less spherical area at the base of the leaves, while those of *P. densus* typically run up the basal leaf margins in a V-shaped pattern to the widest part of the leaf base. The common expression of *P. densus* also differs from *P. luteovirens* in having unbranched stems with a thicker, coarser appearance due to its broader leaves that are closely spaced on the stems, consistently fragile leaf apices, and shorter upper leaf cells. There is a second form of *P. densus* in Central America that is intermediate in aspect, branching, alar cell form, and upper leaf cell length between typical *P. densus* and *P. luteovirens*. Distinguishing *P. luteovirens* from the second expression can be done only by examining the relative development of their alar cells. *Prionodon luteovirens* is here treated in a narrow sense, and all intermediate collections in which the alar cells run up the margins a considerable distance, regardless of whether or not they reach the broadest part of the leaf base, are considered *P. densus*.

Robinson (1967) considered *P. luteovirens* a synonym of *P. dichotomus* because of a confusion over the type specimen of *P. dichotomus* (see Griffin 1973). *Prionodon dichotomus* differs from *P. luteovirens* in having alar cells identical in form and development to those of *P. densus*. It differs from *P. densus* only in having ovate to subcylindrical capsules (similar to those of *P. luteovirens*) rather than globose to oval capsules. *Prionodon dichotomus* is here considered a synonym of *P. densus*.

Excluded taxa

Prionodon hoffmannii Müll. Hal., Hedwigia 40: 56. 1901. Protologue. Costarica, in monte vulcanico de Barba: Dr. C. Hoffmann *1856.*

The type of this species was deposited at B under the herbarium name *Prionodon fragilifolio* Müll. Hal. and presumably was destroyed along with the Berlin herbarium in 1943. It is impossible to determine the identity of this species from its description. Müller compared *P. hoffmannii* to *P. longissimus* and *P. bolivianus* Müll. Hal.; both are synonyms of *P. luteovirens*.

METEORIACEAE

Meteoriaceae Kindb., Gen. Eur. N.-Amer. Bryin. 7. 1897.

Plants small, medium-sized, or robust, green, dull green, yellow green, or golden red, at times jet black tinged. Primary stems at times creeping, irregularly pinnately branched, not stipitate; stems in cross section with enlarged epidermis or sclerodermis present, central strand present, rarely absent; paraphyllia absent; pseudoparaphyllia absent, subfoliose, or foliose, scale leaves present; rhizoids not or rarely branched, from clusters of initials abaxial to the leaf insertions. Secondary stems erect or pendent, irregularly pinnately branched, stem and branch tips often attenuate or stoloniferous. Leaves at times dimorphic or trimorphic, lanceolate, ovate-lanceolate, or ovate-triangular, narrowly elliptic, ovate-acuminate, broadly ovate to orbicular, closely or widely spaced, at times apices twisted when dry, varying from strongly plicate to smooth; margins at times serrulate to serrate or crenulate by projecting papillae, rarely entire; upper marginal cells sometimes forming a more or less distinct border, sometimes decurrent, inserted in a straight or U-shaped line; costae single, usually ending 1/3–2/3 the leaf length, at times ending near the apex, at times ending in a small spine, rarely absent or shortly and inconspicuously double, in cross section cells usually homogeneous, thick-walled, rarely with guide cells and single layer of dorsal and ventral stereid cells; cells smooth, unipapillose, or pluripapillose, papillae seriate or scattered over the cell lumina; upper cells isodiametric, oval, rhombic, fusiform or linear; median cells linear to linear-fusiform or linear flexuose; basal cells across the insertion short-rectangular, more or less enlarged; alar cells weakly or strongly differentiated. Asexual reproduction sometimes by deciduous flagelliform branches or caducous leaves. Dioicous or autoicous. Vaginulae at times densely hairy. Setae mostly elongate, smooth or papillose. Capsules immersed or exserted, erect to inclined, subglobular to ovoid, oblong, ovate-cylindrical, or cylindric-elliptic; stomata rarely absent; exothecial cells with thin or thick walls; opercula obliquely conic to rostrate; annuli rudimentary; peristome diplolepideous; exostome teeth on dorsal (outer) surface cross-striate below, or papillose to smooth throughout; endostome with high or low basal membranes, segments keeled or plane, at times perforate, cilia rudimentary or absent. Spores lightly papillose, uni- or bimodal. Calyptrae cucullate or mitrate, naked or hairy.

The Meteoriaceae were established by Kindberg (1897) for the genera *Papillaria* and *Meteorium*. Brotherus (1906c) expanded the group to include 13 genera, but reduced it to a subfamily of the Neckeraceae. Although Fleischer (1908) considered the family "Eine sehr natürliche Moosgruppe," his treatment of the Meteoriaceae (15 genera in 2 tribes) established it as a morphologically variable group held together mainly by its often pendent life-form and tropical or subtropical distribution.

The Meteoriaceae are usually placed in the Leucodontales (Fleischer 1908; Brotherus 1925; Walther 1983; Vitt 1984). The family, however, has been transferred to the Hypnales (Buck 1994a) and placed near the Brachytheciaceae, partly because its exostome teeth are often horizontally striate at base; it lacks stolon-like primary stems that are tightly adherent to the substrate; and it has greatly reduced stolon leaves. Buck (1994a, 1994b) also reduced the family by transferring *Pilotrichella*, *Orthostichella*, *Weymouthia*, and *Squamidium* to the Lembophyllaceae. Although Allen and Magill (2003) supported the transfer of *Pilotrichella*, *Orthostichella*, and *Weymouthia* into the Lembophyllaceae, they returned *Squamidium* to the Meteoriaceae. Quandt and Huttunen (2004), on the basis of a molecular analysis of pendent mosses, support the transfer of *Weymouthia* into the Lembophyllaceae. Their analysis, however, indicates *Aerolindigia*, *Squamidium*, and *Meteoridium* should be transferred to the Brachytheciaceae. The position of *Orthostichella* in their analysis was unresolved. Quandt and Huttunen did not treat *Pilotrichella* in their study. It seems clear from morphological and molecular evidence that *Aerolindigia* and *Meteoridium* belong in the Brachytheciaceae. On other hand, *Squamidium* is so morphologically different (*e.g.*, linear, entirely papillose exostome teeth, immersed capsules, mitrate calyptra, plants with an intense black coloration, and faint costae), that its placement in the Brachytheciaceae is difficult to accept.

The Meteoriaceae are one of the most challenging families of mosses to characterize. They are predominantly epiphytic, pleurocarpous mosses that commonly grow pendent, and their gametophytes often have an intense blackish coloration. The family typically has creeping stolons with re-

duced leaves, and erect, evenly foliose secondary stems that lack paraphyllia and have a weak central strand. Its rhizoids are not or weakly branched and come from circular clusters of initials at the abaxial side of the leaf insertion. The leaves usually have weak single costae. Its leaf cells are firm-walled, occasionally porose, papillose or smooth, and the basal cells in the alar region vary from strongly differentiated to nearly undifferentiated. The family is dioicous or autoicous, perichaetial leaves are weakly differentiated, capsules are immersed, emergent or long-exserted, and its peristomes are whitish yellow and reduced. The calyptrae are cucullate or mitrate, naked or hairy.

1. Leaf cells smooth 2
1. Leaf cells papillose 6

2. Alar cells well developed, often bulging and inflated . . . . . 7. *Squamidium*
2. Alar cells not or weakly developed, never inflated 3

3. Leaves squarrose to squarrose-recurved . . . . . 11. *Zelometeorium*
3. Leaves erect to erect-spreading from the insertion 4

4. Plants dioicous; axillary hairs with brown basal cells . . . . . 5. *Meteoridium*
4. Plants autoicous; axillary hairs hyaline throughout 5

5. Stems with subfoliose pseudoparaphyllia; setae 4–7 mm long, smooth; exostome teeth papillose; leaves narrowly long-acuminate; median leaf cells to 60–120 × 10–17 µm . . . . . 4. *Lindigia*
5. Stems with scale leaves, pseudoparaphyllia absent; setae 1–4 mm long, scabrous to papillose; exostome teeth cross-striate below; leaves acuminate; median leaf cells 50–70 × 5–8 µm . . . . . 1. *Aerolindigia*

6. Leaf cells pluripapillose, papillae only over the cell walls . . . . . 10. *Trachypus*
6. Leaf cells unipapillose or pluripapillose, papillae over the lumina or over the lumina and lumina and cell walls 7

7. Costa short and double or absent . . . . . 2. *Barbellopsis*
7. Costa single 8

8. Leaf insertions more or less straight . . . . . 6. *Meteorium*
8. Leaf insertions U-shaped 9

9. Leaf cells with 1–2 papillae . . . . . 9. *Trachypodopsis*
9. Leaf cells with 3–7 papillae 10

10. Leaves cordate; basal margins crenulate by projecting papillae; apices tapered to long, slender hair-points, not twisted . . . . . 3. *Floribundaria*
10. Leaves strongly auriculate; basal margins serrate or dentate; apices acuminate, consistently twisted when wet or dry . . . . . 8. *Toloxis*

1. *Aerolindigia* M. Menzel, Nova Hedwigia 52: 321. 1991.

Plants small, slender, in pale green to golden green tufts. Primary stems creeping, irregularly pinnately branched, not stipitate; stems in cross section with one row of somewhat enlarged epidermal cells, subepidermal cells small, red, thick-walled, cortical cells enlarged, firm-walled, central strand weakly developed; paraphyllia and pseudoparaphyllia absent, scale leaves present; rhizoids in dense clusters, dark brown to blackish, smooth, not branched, from clusters of initials abaxial to the leaf insertions. Secondary stems erect or pendent, irregularly pinnately branched; axillary hairs 2-celled, hyaline. Leaves lanceolate to ovate-lanceolate, widely spaced, erect-spreading, twisted when dry, erect-spreading to spreading when wet, gradually acuminate, decurrent, apices often twisted, inserted in a U-shaped line, stem leaves subcordate at base, branch leaves asymmetric at base; margins plane or narrowly recurved at base, serrulate to near the leaf base; costae single, ending 1/3–2/3 the leaf length, in cross section cells homogeneous, thick-walled; cells smooth, upper and median cells lin-

ear-fusiform, thick-walled, not porose; basal cells across the insertion short-rectangular, more or less enlarged; alar cells not or weakly differentiated as a few short-rectangular cells. Autoicous. Gemmate perigonia and perichaetia lateral on secondary stems. Setae elongate, erect, scabrose to papillose throughout. Capsules erect to somewhat inclined, ovate-cylindrical; exothecial cells rounded to subquadrate below the mouth, rectangular below, with thin, wavy walls; stomata on neck; opercula obliquely conic to short-rostrate; annuli rudimentary, of two rows of firm-walled cells; peristome diplolepideous; exostome teeth on dorsal (outer) surface densely cross-striate in lower half, papillose above, ventral (inner) surface smooth, considerably narrower than the dorsal surface; endostome smooth to lightly papillose, as long as the exostome, basal membranes high, segments strongly keeled, perforate, cilia absent. Spores round, lightly papillose, bimodal. Calyptrae cucullate, naked.

Aerolindigia is a monospecific genus of small, slender, epiphytic plants. Its leaves have sharply serrulate margins, weak, single costae, linear-fusiform, smooth leaf cells, and very weakly differentiated alar cells. It is autoicous, and collections nearly always have sporophytes. The capsules are more or less erect and shortly exserted on scabrous or densely papillose setae. The opercula are shortly rostrate, and the exostome teeth horizontally striate on the dorsal surface. The exothecial cells in *Aerolindigia* are variously rectangular and have thin, wavy walls. It has cucullate calyptrae. The genus was segregated from *Lindigia* by Menzel (1991, as *Aerolindigia*) and Visnadi and Allen (1991, as *Rhynchostegiella*); both placed the segregate in the Brachytheciaceae. Recent molecular analyses of the genus (Buck & Goffinet 2000; Goffinet & Buck 2004; Quandt & Huttunen 2004) also place *Aerolindigia* in the Brachytheciaceae.

Lindigia and *Aerolindigia* are gametophytically remarkably similar; *Lindigia* differs primarily in having subfoliose pseudoparaphyllia; longer, smooth setae; papillose exostome teeth; and a more reduced endostome. The peristomial differences between the two genera are well illustrated by SEM micrographs in the revisionary treatments of Menzel (1991) and Visnadi and Allen (1991). Many lectotypificatons were made in these revisions, and at times the lectotypification decisions differ; it may be important to note that the Visnadi and Allen revision was published two months before that of Menzel. The gametophytes of both genera are very close to *Meteoridium*, but that genus is dioicous and has axillary hairs that are brown at base.

The name *Aerolindigia* combines the Greek *aeros* (air) with the generic name *Lindigia*.

Aerolindigia capillacea (Hornsch. *in* Mart.) M. Menzel, Nova Hedwigia 52: 322. 1991. *Pilotrichum capillaceum* Hornsch. *in* Mart., Fl. Bras. 1(2): 58. 1840. *Neckera capillacea* Hornsch. *in* Mart., Fl. Bras. 1(2): 58. 1840, invalid name, lacks a description. *Lindigia capillacea* (Hornsch. *in* Mart.) Hampe *in* Lorentz, Bot. Zeitung (Berlin) 26: 819. 1868. *Meteorium capillaceum* (Hornsch. *in* Mart.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 251. 1877. *Rhynchostegiella capillacea* (Hornsch. *in* Mart.) Visnadi & B. H. Allen, Bryologist 94: 14. 1991. Protologue. [Brazil] Ad radices arborum prope Sebastianopolin, Novembri, c.fr. maturis: *Beyrich*. Types. Brazil. Rio de Janeiro, Corcovado, Nov., *Beyrich* (BM, holotype; BM, isotypes).

Leskea aciculata Taylor, London J. Bot. 6: 339. 1847. *Neckera aciculata* (Taylor) Mitt., Kew J. Bot. 3: 353. 1851. *Meteorium aciculatum* (Taylor) Mitt., J. Linn. Soc., Bot. 12: 448. 1869. *Lindigia aciculata* (Taylor) Hampe, Bot. Zeitung (Berlin) 27: 868. 1869. Protologue. [Ecuador] Near Quito; Prof. W. Jameson. Nov. 1846. Types. Ecuador, near Quito, Nov. 1846, *Jameson* (FH, holotype; BM, isotypes).

Lindigia tenella Hampe *in* Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 248. 1872. Protologue. [Mexico] In monte Orizabensi (*Bourg. n^{o} 2763*, aug. 1866). Type. In monte Orizabensi, Aug. 1866, *Bourgeau 2763* (BM, holotype).

Plants small, slender in soft, pale green to golden green tufts. Primary stems creeping, irregularly pinnately branched, not stipitate; stems in cross section with one row of somewhat enlarged epidermal cells, 2–3 rows of small, red, thick-walled cells, subepidermal cells, cortical cells enlarged, firm-walled, central strand weakly developed; paraphyllia and pseudoparaphyllia absent, scale leaves present; rhizoids in dense clusters, dark brown to blackish, smooth, not branched, from clusters of initials abaxial to the leaf insertions. Secondary stems erect or pendent, irregularly pinnately branched, to 5.5 cm long; axillary hairs 2-celled, hyaline. Stem leaves 1.5–2.0 mm long, branch leaves 1.0–1.4 mm

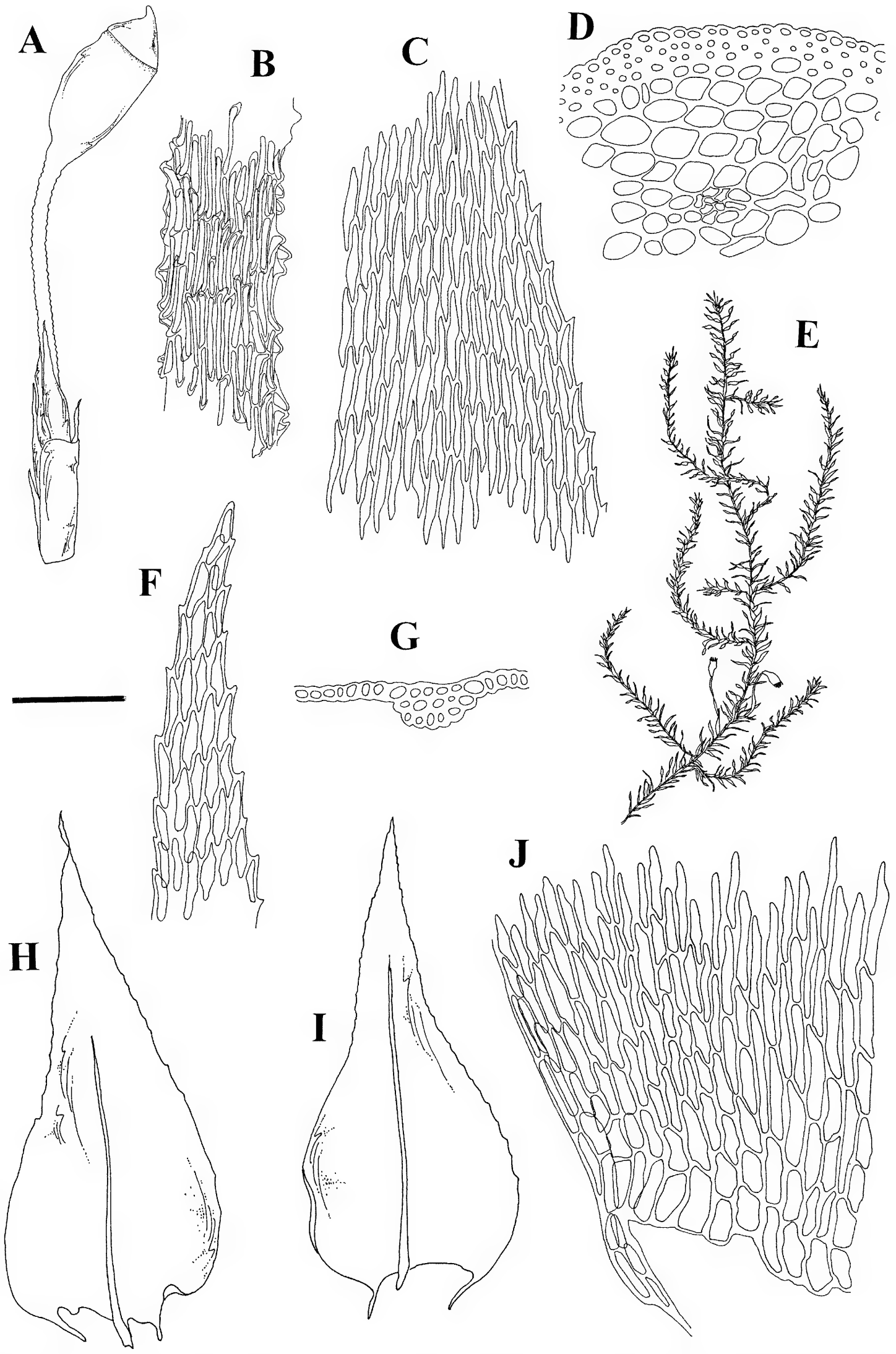
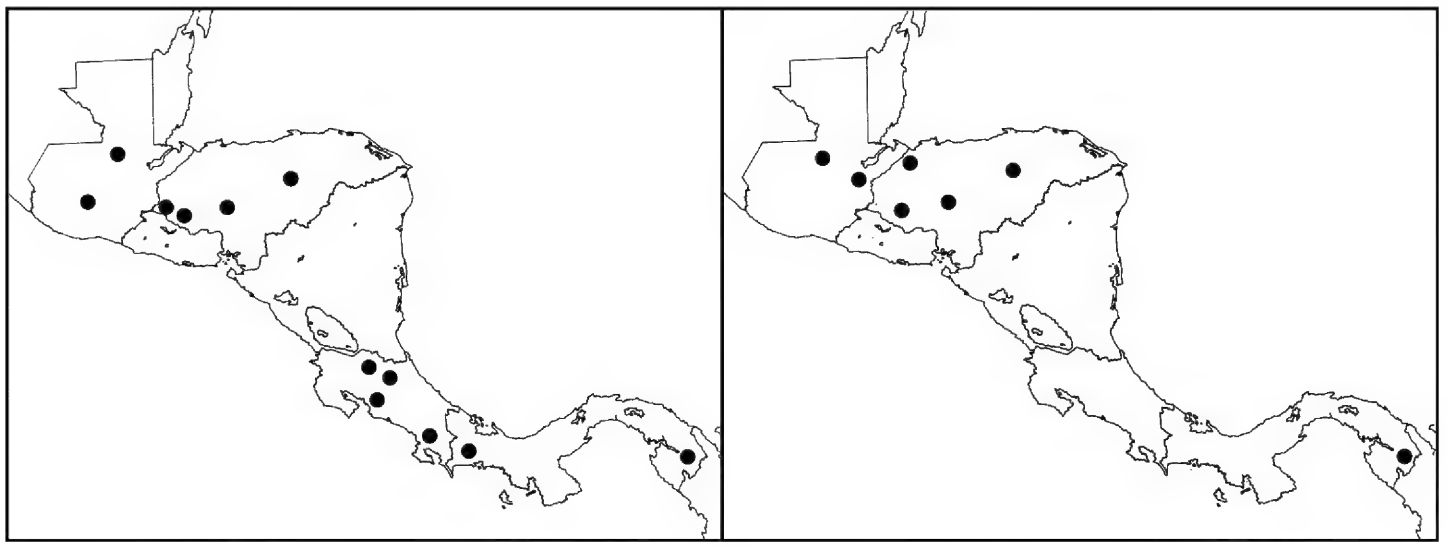


Figure 33. *Aerolindigia capillacea*. A. Sporophyte. B. Seta. C. Median leaf cells. D. Stem in cross section. E. Habit. F. Leaf apex. G. Costa in cross section. H & I. Leaves. J. Basal leaf cells. Scale in mm: bar = 0.06 (C, D, F, G, J); bar = 0.08 (B); bar = 0.41 (H, I); bar = 0.9 (A); bar = 6.4 (E). B from *Griffin 17*; all other figure parts from *Allen 11380*.



Aerolindigia capillacea *Barbellopsis trichophora*

long, lanceolate to ovate-lanceolate, widely spaced, erect-spreading, twisted when dry, apices often twisted, erect-spreading to spreading when wet, gradually acuminate, decurrent, inserted in a U-shaped line, stem leaves subcordate at base, branch leaves asymmetric at base; margins plane or narrowly recurved at base, serrulate to near the leaf base; costae single, ending 1/3–2/3 the leaf length, in cross section cells homogeneous, thick-walled; cells smooth, upper and median cells linear-fusiform, thick-walled, not porose, 50–70 × 5–8 µm; basal cells across the insertion short-rectangular, more or less enlarged; alar cells not or weakly differentiated as a few short-rectangular cells. Autoicous. Gemmate perigonia and perichaetia lateral on secondary stems. Setae elongate, erect, scabrose to papillose throughout, yellowish to red, 1–4 mm long. Capsules erect to somewhat inclined, ovate-cylindrical, 1–1.3 mm long; exothecial cells rounded to subquadrate below the mouth, rectangular below, with thin, wavy walls; stomata on neck; opercula obliquely conic to short-rostrate, 0.5 mm long; annuli rudimentary, of two rows of firm-walled cells; peristome diplolepideous; exostome teeth reddish brown, narrowly triangular, dorsal (outer) surface densely cross-striate in lower half, papillose above, ventral (inner) surface smooth, considerably narrower than the dorsal surface; endostome yellow, smooth to lightly papillose, as long as the exostome, basal membranes high, segments strongly keeled, perforate, cilia absent. Spores round, lightly papillose, bimodal: 10–15 µm and 20–30 µm. Calyptrae cucullate, smooth, 1 mm long.

Illustrations. Bartram (1949, Fig. 120 D–F); Sharp *et al.* (1994, Fig. 703); Churchill and Linares (1995, Fig. 16 a–e); Visnadi and Allen (1991, Figs. 31–34); Menzel (1991, Pl. 2 1–4, Pl. 3 1–3, Pl. 4, Pl. 5); Buck (1998, Pl. 100 1–7); Gradstein *et al.* (2001, Fig. 91 A–E). Figure 33.

Habitat. On leaves, vines, twigs, sticks, trunks of treelets, and on palm nodes, often pendent; 685–3300 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: *Standley 90368* (F, FH); Chimaltenango: *Standley 62030c* (FH). HONDURAS. Comayagua: *Olson 84-31* (MO); Lempira: *Allen 11414* (MO); Ocotepeque: *Allen 14450* (MO); Olancho: *Allen 12496* (MO). COSTA RICA. Alajuela: *Crosby & Crosby 6285* (MO); Heredia: *Crosby & Crosby 6482* (MO); Puntarenas: *Dauphin 1492* (MO); San José: *Crosby & Crosby 6222* (MO). PANAMA. Chiriquí: *Hammel 7429B* (MO); Darién: *Williams 1055* (F, NY).

World range: Mexico, Central America; Caribbean; Western, Northern, and Southern South America, Brazil; West Central and East Tropical Africa, Western Indian Ocean.

Aerolindigia capillacea is an epiphytic species commonly found on twigs or sticks in very moist places. The plants have an odd aspect in the field, because the stems grow horizontally or pendent, with the sporophytes projecting downward rather than upward. *Aerolindigia capillacea* has spreading, decurrent stem leaves that are serrulate throughout and have weak, single costae. The leaf cells are linear-fusiform nearly throughout, with alar cells either not or weakly differentiated, and enlarged, rectangular cells across the leaf base. The branch leaves in *A. capillacea* are flattened when wet and

curiously asymmetric at base, because one side of the leaf base more or less clasps the branch. The leaves often have twisted apices.

The sporophytes of *A. capillacea* have short, densely papillose setae and exserted, more or less erect capsules with obliquely short-rostrate opercula. The peristome of *A. capillacea* is hypnoid in form, with exostome teeth that are strongly cross-striate on the outer surface, which is also considerably broader than the inner surface. The endostome is well formed with a high basal membrane and strongly keeled, perforate segments, but cilia are absent.

Rhynchostegium scariosum (Taylor) A. Jaeger often grows mixed with *A. capillacea*, and the two species are gametophytically almost identical. It differs from *A. capillacea* in having longer (13–15 mm vs. 1–4 mm), smooth setae, long-rostrate opercula, and endostomial cilia. *Lindigia debilis* (Wilson *ex* Mitt.) A. Jaeger is also gametophytically close to *A. capillacea*. It differs, however, in having very long, narrowly acuminate leaves with more sharply serrate margins, and relatively broader and longer median leaf cells. In addition, its stems have subfoliose pseudoparaphyllia. The sporophytes of *L. debilis* differ from those of *A. capillacea* in having longer (4–7 mm), smooth setae, shortly beaked opercula, and linear exostome teeth that are papillose throughout.

2. *Barbellopsis* Broth. *in* Hand.-Mazz., Symb. Sin. 4: 83. 1929.

Barbella sect. *Dicladiella* M. Fleisch., Musci Buitenzorg 3: 805. 1908. *Dicladiella* (M. Fleisch.) W. R. Buck, J. Hattori Bot. Lab. 75: 57. 1994.

Plants medium-sized to robust, in green, yellow green, or golden brown, pendent masses. Primary stems creeping, irregularly branched; stems in cross section with sclerodermis, enlarged, thin-walled cortical cells, central strand small; paraphyllia absent; pseudoparaphyllia foliose; rhizoids red brown, smooth, not branched or sparsely branched from clusters of initials abaxial to the leaf insertions. Secondary stems pendent, irregularly branched, leaves complanate; secondary stem and branch tips often transformed to stoloniferous stems. Primary stem and stoloniferous leaves appressed, lanceolate, auriculate, with flexuose hair-points; secondary stem and branch leaves complanate, wide-spreading, lanceolate to ovate-lanceolate, convolute-concave, decurrent; margins serrulate, plane; costa absent or shortly and inconspicuously double; cells linear, thin-walled, smooth or inconspicuously unipapillose; alar cells short-rectangular to subquadrate, thin-walled or thick-walled, porose. Dioicous. Sporophytes not seen, description from Noguchi (1989) and Buck (1998). Setae short, geniculate to flexuose, smooth or papillose above. Capsules erect, oblong to short-cylindric; exothecial cells short-rectangular, firm-walled, not collenchymatous; stomata absent; opercula long- or conic-rostrate; annuli rudimentary of 1–2 rows of small, firm-walled cells; peristome diplolepideous, yellow, brown when old; exostome teeth linear, horizontally striate below, papillose above; endostome smooth or papillose, basal membranes high, segments keeled and perforate, cilia rudimentary. Spores round, papillose. Calyptrae mitrate, naked.

Barbellopsis is a segregate genus of *Barbella* with two species: *B. trichophora* (Mont.) W. R. Buck and *B. macroblasta* (Broth.) B. H. Allen, *comb. nov.* (basionym: *Barbella marcroblasta* Broth., Philip. J. Sci. 8: 79. 1913). Brotherus (1929) considered *Barbellopsis* distinct from *Barbella* because of the numerous quadrate alar cells in its leaves. Buck (1994a, as *Dicladiella*) more precisely circumscribed the genus: branches complanate-foliate; leaves ecostate with a straight leaf insertion; alar cells well differentiated; annuli rudimentary; exostome teeth cross-striate on the dorsal surface; and calyptrae mitrate. This circumscription is somewhat compromised because Central American collections of *Barbellopsis trichophora* have a short U-shape rather than a straight leaf attachment, and there are species of *Neodicladiella* (another *Barbella* segregate) with complanate-foliate branches and very well-developed alar cells. Nevertheless, *Barbellopsis* appears well founded on the basis of its ecostate leaves (occasionally very short and double), cross-striate exostome teeth, and mitrate calyptrae.

The name *Barbellopsis* combines the generic name *Barbella* with the Greek *opsis* (aspect or appearance).

Barbellopsis trichophora (Mont.) W. R. Buck, Mem. New York. Bot. Gard. 82: 265. 1998. *Isothecium trichophorum* Mont., Ann. Sci. Nat., Bot. sér. 2, 19: 238. 1843. *Neckera trichophora* (Mont.) Müll. Hal., Syn. Musc. Frond. 2: 130. 1850. *Meteorium trichophorum* (Mont.) Sull., U.S. Expl.

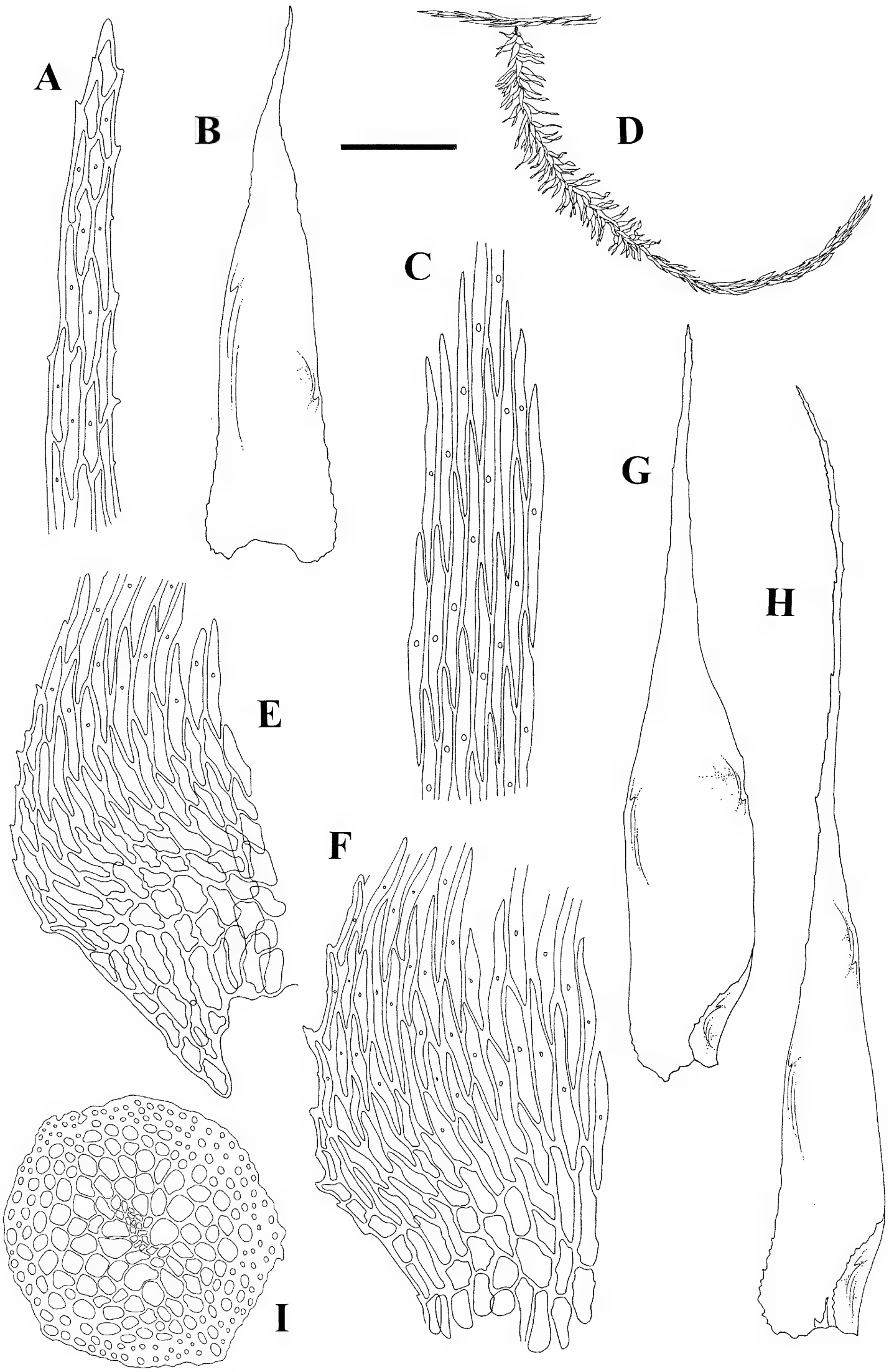


Figure 34. *Barbellopsis trichophora*. A. Leaf apex. B & G. Leaves. C. Median leaf cells. D. Habit. E. Basal cells branch leaf. F. Basal cells stem leaf. H. Stoloniferous leaf. I. Stem in cross section. Scale in mm: bar = 0.06 (A, C, E, F); bar = 0.08 (I); bar = 0.5 (B, G, H); bar = 8 (D). All figure parts from *Allen 12787*.

Exped., Musci 22. 1859. *Pilotrichella trichophora* (Mont.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 259. 1877. *Barbella trichophora* (Mont.) M. Fleisch. *ex* Broth., Nat. Pflanzenfam. I(3): 824. 1906. *Dicladiella trichophora* (Mont.) Redf. & B. C. Tan, Trop. Bryol. 10: 66. 1995. Protologue. [Hawaii] Ad corticem *Radulae reflexae* N. et M. consors, in insulis Sandwich à celeb. *Gaudichaud inventum*. Types (see Streimann 1993). PC, holotype; BM, isotype.

Meteorium cubense Mitt., J. Linn. Soc., Bot. 12: 435. 1869. *Pilotrichella cubensis* (Mitt.) Paris, Index Bryol. 943. 1897. *Squamidium cubense* (Mitt.) Broth., Nat. Pflanzenfam. I(3): 809. 1906. *Barbella cubensis* (Mitt.) Broth., Nat. Pflanzenfam. I(3): 824. 1906. *Dicladiella cubensis* (Mitt.) W. R. Buck, J. Hattori Bot. Lab. 75: 57. 1994. Protologue. Ins. Cuba, *Wright, n. 82*.

Meteorium diclados Schimp. *ex* Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 227. 1872. *Barbella diclados* (Besch.) Broth., Nat. Pflanzenfam. I(3): 824. 1906. Protologue. [Mexico] Mejico, Oajaca (*Galeotti n°* 6885, in herb. Mus. Paris); Cordova (*Bourgeau*).

Leskea heteroclados Schimp. *ex* Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 227. 1872, invalid name, cited in synonymy.

Meteorium enerve Thwaites & Mitt. *ex* Mitt., J. Linn. Soc., Bot. 13: 317. 1873. *Barbella enervis* (Mitt.) M. Fleisch. *ex* Broth., Nat. Pflanzenfam. I(3): 824. 1906. Protologue. Ins. Ceylon. *Dr. Thwaites*. Type (see Streimann 1991). *Thwaites 208* (NY, holotype).

Neckera trichophoroides Hampe, Linnaea 38: 668. 1874. *Pilotrichella trichophoroides* (Hampe) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 259. 1877. *Meteorium trichophoroides* (Hampe) Mitt., Trans. Roy. Soc. Victoria 19: 82. 1882. *Barbella trichophoroides* (Hampe) Broth., Nat. Pflanzenfam. I(3): 284. 1906. Protologue. Lord Howe's Island, Summit of Mount Gower. Type. Lord Howe's Island, Summit Mount Gower (S, isotype).

Plants medium-sized to robust, in green, yellow green, or golden brown, soft, pendent masses. Primary stems creeping; secondary stems pendent, to 20 cm long, irregularly branched, complanate-foliate, secondary stem and branch tips often transformed to stoloniferous stems; stems in cross section with sclerodermis of 3–5 rows of small, red brown, thick-walled cells, cortical cells enlarged, hyaline, thin-walled, central strand small; paraphyllia absent; pseudoparaphyllia foliose; rhizoids red brown, smooth, not branched or sparsely branched, from clusters of initials abaxial to the leaf insertions, developed only when stems and branches touch the substrate. Primary stem and stoloniferous leaves appressed, lanceolate, auriculate, 2.5–4.0 mm long, flexuose hair-pointed, convolute-concave, decurrent; margins plane, serrulate throughout or serrate to irregularly dentate near the leaf base; costa none or shortly and inconspicuously single or double; cells linear, 100–134 × 4–6 µm, thin-walled, smooth or inconspicuously unipapillose; alar cells short-rectangular to subquadrate, thin-walled. Secondary stems and branches complanate-foliate, leaves wide-spreading, lanceolate to ovate-lanceolate, rounded to weakly auriculate, 2–3 mm long, gradually acuminate, not hair-pointed, shortly decurrent; margins plane, serrulate throughout or serrate to irregularly dentate near the leaf base; costa absent or short and double; cells linear, 80–120 × 4–6 µm, smooth or unipapillose over the cell lumina, thin-walled; alar cells subquadrate to short-rectangular, thick-walled, porose. Dioicous. Perichaetia lateral, gemmate, 1 mm long, paraphyses absent. Sporophytes unknown from Central America.

Illustrations. Brotherus (1929, Pl. 2 10–13); Bartram (1933a, Fig. 127); Bartram (1939, Pl. 17 283); Bartram (1949, Fig. 121 A–D); Gangulee (1976, Fig. 647); Li Xing-jiang (1985, Pl. 116 6–9); Norris and Koponen (1985, Fig. 15 e–g); Noguchi (1989, Fig. 229); Streimann (1991, Figs. 65–70); Sharp *et al.* (1994, Fig. 542 d–h); Churchill and Linares (1995, Fig. 121 a–f); Duarte Bello (1997, Pl. 194); Buck (1998, Pl. 102 1–7); Wu and Wang (2000, Pl. 214 5–8). Figure 34.

Habitat. Pendent from leaves, vines, twigs, and tree limbs; 1000–2600 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: *Standley 71668* (F, FH); Zacapa: *Steyermark 42797* (F, FH). HONDURAS. Comayagua: *Allen 13961* (MO); Cortés: *Allen 14172* (MO, TEFH); Lempira: *Allen 11422* (MO, TEFH); Olancho: *Allen 12590* (MO, TEFH). PANAMA. Darién: *Mori & Gentry 4419* (MO).

World range: Mexico; Central America; Caribbean; Western South America; China, Eastern Asia; Indian Subcontinent, Indo-China, Malesia; Australia (including Lord Howe Island); North-Central and Southwestern Pacific.

Barbellopsis trichophora is a moderate to high elevation cloud forest species that grows in pendent masses from twigs or branches. It has a distinctive look in the field, because its complanate-foliate secondary stems and branches are elongate at the tips into long, stoloniferous shoots with imbricate, long, hair-pointed leaves. The leaves of *B. trichophora* are weakly decurrent, and either ecostate or have short, inconspicuously single or double costae. Its leaf margins are serrulate throughout, with marginal teeth more pronounced at the extreme base. The extremely long, thin-walled leaf cells of *B. trichophora* are an especially notable feature; they are either inconspicuously unipapillose or smooth.

Streimann (1991 as *Barbella cubensis*, 1993) described in detail the morphology of *Barbellopsis trichophora* and discussed its morphological variation. These treatments also give the complete synonymy of the species and its world distribution.

3. *Floribundaria* M. Fleisch., Hedwigia 44: 301. 1905.

Papillaria sect. *Floribundaria* Müll. Hal., Linnaea 35: 267. 1867, invalid name, lacks a description.
Floribundaria sect. *Eufloribundaria* Broth., Nat. Pflanzenfam. I(3): 821. 1906, illegitimate name.

Plants small and slender, in pendent masses. Stems irregularly to pinnately branched, not stipitate; stems in cross section with sclerodermis, enlarged cortical cells, and weakly developed central strand; paraphyllia and pseudoparaphyllia absent, scale leaves present; rhizoids sparsely developed, when present reddish brown, smooth, not or rarely branched, from clusters of initials abaxial to the leaf insertions; axillary hairs with 1–2 short, subquadrate basal cells and 3–4 short, rounded, hyaline upper cells. Stem and branch leaves lanceolate, somewhat ovate and strongly clasping at base. Leaves widely spaced, erect-spreading to spreading and twisted when dry, erect-spreading when wet, gradually tapered to long, slender hair-points, plane, smooth, cordate at base, slightly decurrent; margins plane, serrulate to serrate above, crenulate by projecting papillae below; costae single, ending at or a little above midleaf, in cross section consisting of homogeneous, thick-walled cells; cells seriate-papillose with 3–5 papillae over the cell lumina and/or cell walls, upper and median cells linear, firm-walled; basal cells oblong to rectangular, smooth and porose; alar cells not differentiated. Dioicous. Setae short, smooth or variously roughened. Capsule short-exserted, erect, symmetric ovoid to oblong; stomata present; opercula obliquely short conic-rostrate; peristome double; exostome teeth on dorsal (outer) surface cross-striate below, papillose above; endostome basal membranes medium to high, segments narrow, keeled, perforate, cilia absent or rudimentary. Calyptrae cucullate, hairy.

Floribundaria was established by Fleischer (1905a) for 12 species, most of which were previously placed in *Papillaria* or *Meteorium*. He later (Fleischer 1908) divided the genus into two sections (*Floribundaria* and *Trachycladiella* Fleisch.), but these were considered unnatural (Noguchi 1976; Norris & Koponen 1985) due to significant sectional differences in calyptral form and leaf cell ornamentation. Menzel (Menzel & Schultze-Motel 1994) recognized *Trachycladiella* (Fleisch.) M. Menzel as a genus of two species restricted to Southeast Asia and Japan.

At present *Floribundaria* is a mostly tropical genus of 13 species. The genus has slender, often pendent plants with more or less complanate leaves that are widely spaced on the stems. Its leaves are variously clasping at base and have long narrow cells with papillae over the cell lumina as well as the cell walls. The upper leaf margins in *Floribundaria* are variously serrate to serrulate and its weak, single costae typically end at midleaf. Distinctive sporophytic features of *Floribundaria* include its short, smooth to variously roughened setae, exostome teeth cross-striate on the outer surface, and absent to rudimentary endostomial cilia. The calyptrae in *Floribundaria* are cucullate and hairy.

It is difficult to distinguish *Floribundaria* from the extremely variable *Meteorium*. The best way to separate the two genera is by their leaf insertions: U-shaped in *Floribundaria*, straight in *Meteorium*. In Central America, *Meteorium* also differs from *Floribundaria* in having crenulate rather than serrulate to serrate upper leaf margins. *Toloxis* is somewhat similar to *Floribundaria* in leaf shape, and both genera have U-shaped leaf insertions as well as pluripapillose leaf cells. In Central America, it differs from *Floribundaria* in having acuminate leaf apices that are strongly twisted when wet or dry and auriculate leaf bases that are serrate to dentate on the basal margins.

The name *Floribundaria* combines the Latin adjective *floribundus* (profusely flowering) with the substantival suffix *-arium* (indicating a place where something is done or a container). As a whole the genus *Floribundaria* rarely has sporophytes; however, the generic name is based on *Papillaria floribunda* (Dozy & Molk.) Müll. Hal., which in Java and New Guinea (see Norris & Koponen 1985) is frequently fertile.

Floribundaria flaccida (Mitt.) Broth., Nat. Pflanzenfam. I(3): 822. 1906. *Meteorium flaccidum* Mitt., J. Linn. Soc., Bot. 12: 443. 1869. *Papillaria flaccida* (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 267. 1877. Protologue. Andes Peruvianae, in monte Guayrapurina (3000 ped.), *Spruce, n. 1191.*

Plants small and slender, in dull green or yellow green, pendent masses. Stems irregularly to pinnately branched, not stipitate, to 10 cm long; stems in cross section with sclerodermis of 2–4 rows of small, yellow or red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, firm-walled, central strand weakly developed; paraphyllia and pseudoparaphyllia absent, scale leaves present; rhizoids sparsely developed, when present reddish brown, smooth, not or rarely branched, from clusters of initials abaxial to the leaf insertions; axillary hairs with 1–2 short, subquadrate, basal cells and 3–4 short, rounded, hyaline upper cells. Stem and branch leaves widely spaced, erect-spreading to spreading and twisted when dry, erect-spreading when wet, lanceolate with a somewhat ovate, strongly clasping base, 1.6–2.0 mm long, gradually tapered to long, slender hair-points, plane, smooth, cordate at base, slightly decurrent; margins plane, serrulate to serrate above, crenulate by projecting papillae below; costae single, ending at or a little above midleaf, in cross section consisting of homogeneous, thick-walled cells; cells seriate-papillose with 3–5 papillae over the cell lumina and/or cell walls, upper and median cells linear, firm-walled, 40–80 × 3–4 µm; basal cells oblong to rectangular, 20–50 × 5–10 µm, smooth and porose; alar cells not differentiated. Dioicous. Sporophytes not seen.

Illustrations. Churchill and Linares (1995, Fig. 121 g–h, as *F. usneoides*); Gradstein *et al.* (2001, Fig. 154 G). Figure 35.

Habitat. Epiphytic; 975–1153 m.

Distribution in Central America. GUATEMALA. Chimaltenango: *Bequaert 70* (FH). COSTA RICA. Alajuela: *Brenes 19079* (F, FH); San José: *Valerio 152* (FH, US).

World range: Central America; Western, Northern, and Southern South America, Brazil.

Floribundaria flaccida is a very slender moss that grows in soft mats with long pendent stems and branches. It has narrowly ovate-lanceolate leaves with capillary hair-points that are widely spaced on the stems and erect-spreading to spreading from a strongly clasping base. The upper and median leaf cells are linear, and they have 3–5 papillae seriately arranged over the cell walls and lumina. The leaves of *F. flaccida* have undifferentiated or slightly differentiated alar cells, and the upper margins are distinctly serrate to serrulate.

Central American material of *F. flaccida* was originally named *Meteorium deppei*, which is a remarkably variable species. The form of *M. deppei* most similar to *F. flaccida* has extremely slender, pendent plants with hair-pointed leaves. The leaves of this *M. deppei* form are also similar to those of *F. flaccida* in size, shape, and in having strongly clasping bases. This slender form of *M. deppei* differs from *F. flaccida* in having closely spaced leaves that overlap at base. In contrast, the leaves of *F. flaccida* are so widely spaced that the leaf insertions can clearly be seen on the stems without dissecting the leaves. Furthermore, the leaf margins in *M. deppei* are never serrate, but rather crenulate throughout by projecting papillae, and the alar cells are weakly but distinctly differentiated.

Gradstein *et al.* (2001) attributed only *F. flaccida* to the Neotropics. Buck (2003) also used that name for material from French Guiana, but noted some material from there had the short leaf apices typically found in *F. floribunda* (Dozy & Molk.) M. Fleisch. There are, in MO, two collections of *F. floribunda* (*Buck 33283, 33319*) from French Guiana. Florschütz-de Waard (1990) reported *F. floribunda* from Suriname and French Guiana; however, the Suriname material of *Floribundaria* I examined (*Florschütz-de Waard & Florschütz 4794*, F, MO) is *F. flaccida*. Britton (1913) erroneously synonymized *Floribundaria flaccida* with *Zelometeorium patulum*.

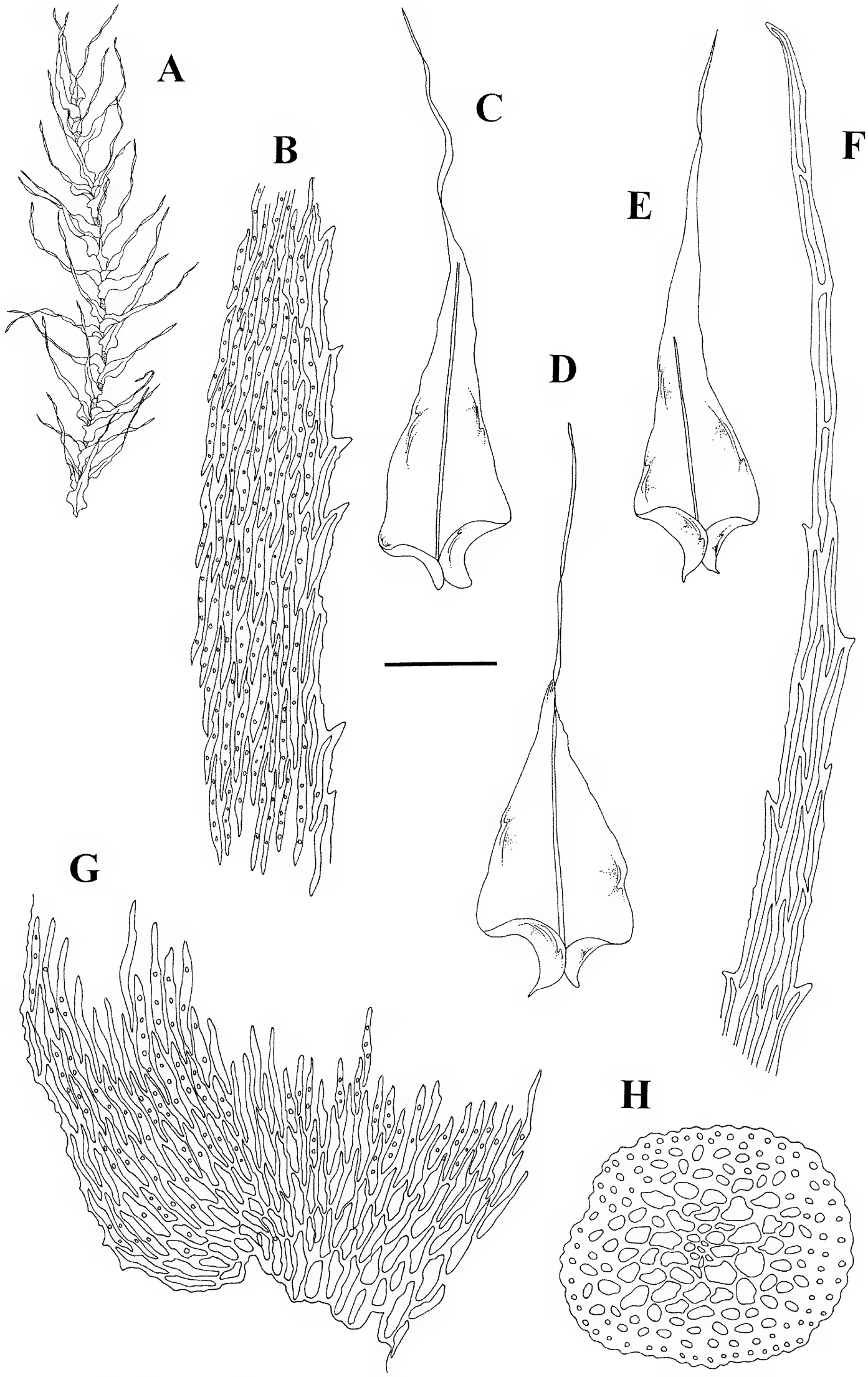
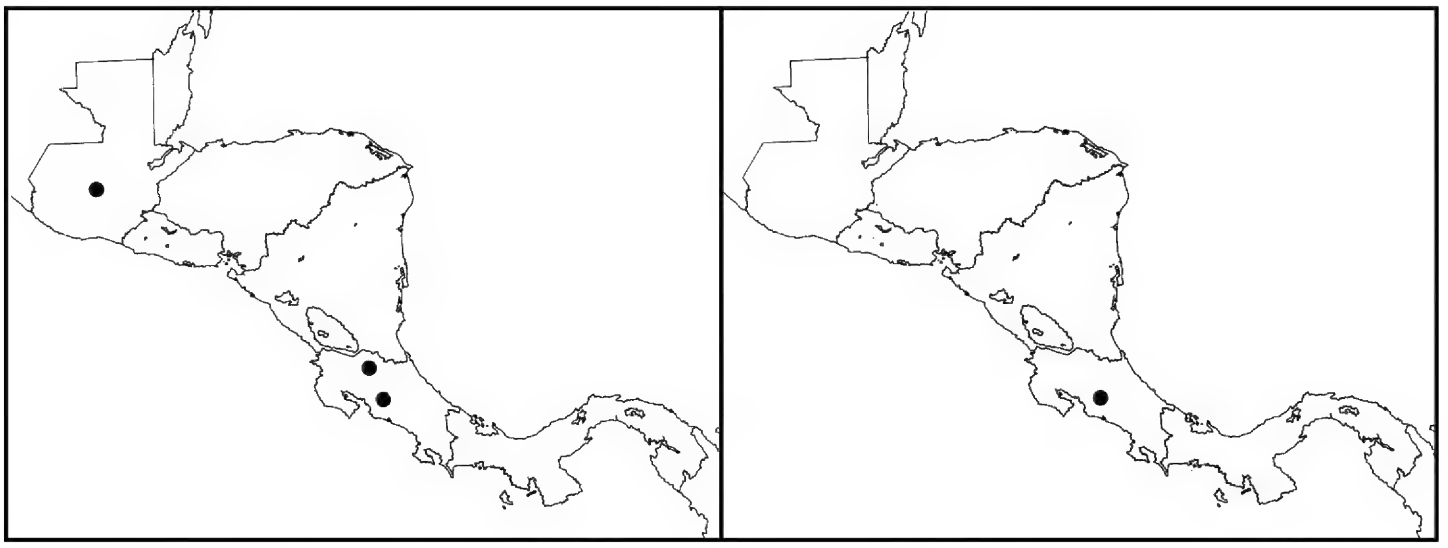


Figure 35. *Floribundaria flaccida*. A. Habit. B. Median leaf cells and margin. C–E. Leaves. F. Leaf apex. G. Basal leaf cells. H. Stem in cross section. Scale in mm: bar = 0.05 (B, F–H); bar = 0.5 (C–E); bar = 1.96 (A). All figure parts from *Valerio 152*.



Floribundaria flaccida *Lindigia debilis*

4. *Lindigia* Hampe, Linnaea 31: 527. 1862.

Plants small, slender, in soft, green to golden green tufts. Stems creeping, irregularly pinnately branched, not stipitate, stem and branch leaves not differentiated; stems in cross section with several rows of orange red, thick-walled epidermal cells, enlarged, thin-walled cortical cells, central strand weakly developed; paraphyllia absent; pseudoparaphyllia subfoliose; rhizoids smooth, not branched, from clusters of initials abaxial to the leaf insertions; axillary hairs 4-celled, all hyaline. Leaves ovate-lanceolate, widely spaced, irregularly spreading to erect, frequently twisted above, slenderly acuminate to hair-pointed, decurrent; margins plane, serrulate to weakly denticulate; costae single, ending 1/4–1/3 the leaf length, in cross section cells homogeneous, thick-walled; cells smooth, upper and median cells fusiform, oblong- to linear-rhombic, thick-walled, often porose; basal cells across the insertion short-rectangular, more or less enlarged; alar cells not or weakly differentiated as a few short-rectangular cells. Autoicous. Setae elongate, erect, smooth. Capsules erect to curved, cylindric-elliptic; exothecial cells irregularly quadrate below the mouth, irregularly rectangular below, with moderately thick walls; stomata on neck; opercula conical, short-rostrate; annuli rudimentary, of one row of firm-walled cells; peristome diplolepideous; exostome teeth narrowly triangular, dorsal (outer) surface densely papillose throughout, ventral (inner) surface weakly papillose; endostome papillose, as long as the exostome, basal membranes high, segments not keeled or perforate, cilia absent. Spores round, lightly papillose. Calyptrae cucullate, smooth.

Lindigia is a monospecific genus of small, slender, epiphytic plants. It has stems with subfoliose pseudoparaphyllia, and sharply serrulate leaves with weak, single costae, fusiform, smooth leaf cells, and weakly differentiated alar cells. It is autoicous and collections usually have sporophytes. The capsules are more or less erect and shortly exserted on smooth setae. The opercula are conic-rostrate, the narrow exostome teeth are papillose throughout, and the endostome segments are narrow and neither keeled nor perforate. Excellent SEM illustrations of the exostome and endostome in *Lindigia* were published by Menzel (1991) and Visnadi and Allen (1991). The calyptrae in *Lindigia* are cucullate.

The genus was revised by Menzel (1991) and Visnadi and Allen (1991). These treatments retained *Lindigia* in the Meteoriaceae, and both failed to note the presence of subfoliose pseudoparaphyllia in the genus. Allen (1987f) in noting the presence of subfoliose pseudoparaphyllia in *Lindigia* considered them unusual, because the leaf cells are thin-walled and swollen in the same manner as those of *Vesicularia* (Müll. Hal.) Müll. Hal. *Lindigia* is the only genus in the Meteoriaceae to have such structures. Indeed, the combination of its smooth leaf cells and odd subfoliose pseudoparaphyllia seem to indicate the genus is misplaced in the Meteoriaceae. *Lindigia* has been put in the Brachytheciaceae (Buck & Goffinet 2000; Goffinet & Buck 2004); however, its strange pseudoparaphyllia and *Leucodon*-type peristome argue against such a placement. The overall characteristics of *Lindigia* make it difficult to place in any existing family.

The name *Lindigia* honors Alexander (Alejandro) Lindig, a plant collector living in Bogotá, Colombia, between "at least" 1859 and 1863 (Sayre 1975).

Lindigia debilis (Wilson *ex* Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1876–77: 313. 1878. *Neckera debilis* Wilson *ex* Mitt., Kew J. Bot. 3: 352. 1851. *Meteorium debile* (Wilson *ex* Mitt.) Mitt., J. Linn. Soc., Bot. 12: 448. 1869. Protologue. [Ecuador] In vicinity of Quito, *Jameson 64*. Types (see Visnadi & Allen 1991). BM, holotype; BM, FH, MICH, isotypes.

Leskea debilis Wilson *ex* Mitt., Kew J. Bot. 3: 352. 1851, invalid name, lacks a description.

Lindigia curtipes Hampe, Linnaea 31: 528. 1862. Protologue. [Colombia] Cipacon, Aug. 1861, *Lindig 2016*. Types (see Visnadi & Allen 1991). BM, holotype; BM, FH, H, NY, US, isotypes.

Lindigia pilotrichelloides Hampe, Ann. Sci. Nat., Bot. sér. 5, 4: 376. 1865, illegitimate name, includes a previously described species.

Eriodon brevisetus E. B. Bartram, Rev. Bryol. Lichénol. 6: 16. 1933 [1934]. Protologue. [Ecuador] Banks of River Napo, 1869, *Villavicentia 139*. Type (see Visnadi & Allen 1991). FH, holotype.

Plants small, slender, in soft, green to golden green tufts. Stems at times creeping, to 20 cm long, irregularly pinnately branched, not stipitate, stem and branch leaves not differentiated; stems in cross section with several rows of orange red, thick-walled epidermal cells, enlarged, thin-walled cortical cells, central strand weakly developed; paraphyllia absent; pseudoparaphyllia foliose; rhizoids reddish orange, smooth, not branched, from clusters of initials abaxial to the leaf insertions; axillary hairs 4-celled, all hyaline. Stem leaves 2.9–3.4 mm long, branch leaves 1.7–3.0 mm long, ovate-lanceolate, widely spaced, irregularly spreading to erect, frequently twisted above, slenderly acuminate to hair-pointed, not to weakly decurrent; margins plane, serrulate to weakly denticulate; costae single, ending 1/4–1/3 the leaf length, in cross section cells homogeneous, thick-walled; cells smooth, upper and median cells fusiform, oblong- to linear-rhombic, thick-walled, often porose, 60–120 × 10–17 µm; basal cells across the insertion short-rectangular, more or less enlarged; alar cells not or weakly differentiated as a few short-rectangular cells. Autoicous. Setae elongate, erect, smooth, orange to red, 3–6(–9) mm long. Capsules erect to curved, cylindric-elliptic, 1–2 mm long; exothecial cells irregularly quadrate below the mouth, irregularly rectangular below, with moderately thick walls; stomata on neck; opercula conical, short-rostrate, 0.3–0.5 mm long; annuli rudimentary, one row firm-walled cells; peristome diplolepideous; exostome teeth yellow, narrowly triangular, dorsal (outer) surface densely papillose throughout, ventral (inner) surface weakly papillose; endostome yellow, papillose, as long as the exostome, basal membranes high, segments not keeled, not perforate, cilia absent. Spores round, lightly papillose, 15–25 µm. Calyptrae cucullate, smooth, 1.0–1.5 mm long.

Illustrations. Churchill and Linares (1995, Fig. 122 a–d); Visnadi and Allen (1991, Figs. 2–30); Menzel (1991, Pl. 1, Pl. 2 5–8, Pl. 3 4–6); Gradstein *et al.* (2001, Fig. 155 A–D). Figure 36.

Habitat. Epiphytic on tree trunks and branches, rarely on rocks; 2100–3200 m.

Distribution in Central America. COSTA RICA. San José: *Griffin et al. 539* (FLAS).

World range: Central America; Western and Northern South America.

In its typical expression *Lindigia debilis* has well-spaced, laxly spreading leaves with twisted apices. The ovate-lanceolate leaves are rounded at base, serrulate to denticulate, and have very long, narrow apices. Occasionally the leaves may be erect, closely spaced, and weakly or not twisted at the apex. At the other extreme plants may have leaves so widely spaced that consecutive leaves do not overlap. The sporophytes of *L. debilis* have smooth setae and more or less erect, cylindric to elliptic capsules with conic-rostrate opercula. *Lindigia debilis* has a *Leucodon*-type exostome with teeth that are narrow and papillose throughout. The endostome is well formed with a high basal membrane, but the processes are narrow, flat, not perforate, and cilia are absent.

Lindigia debilis is gametophytically difficult to distinguish from *Aerolindigia capillacea*. The oblong-lanceolate leaves of *A. capillacea*, however, are somewhat smaller than those of *L. debilis*, and they are more broadly acuminate. Furthermore, the leaf margins in *A. capillacea* are less strongly serrulate, the median leaf cells are narrower and shorter than those of *L. debilis*, and the stems lack pseudoparaphyllia. The sporophytes of *A. capillacea* differ from those of *L. debilis* in having shorter

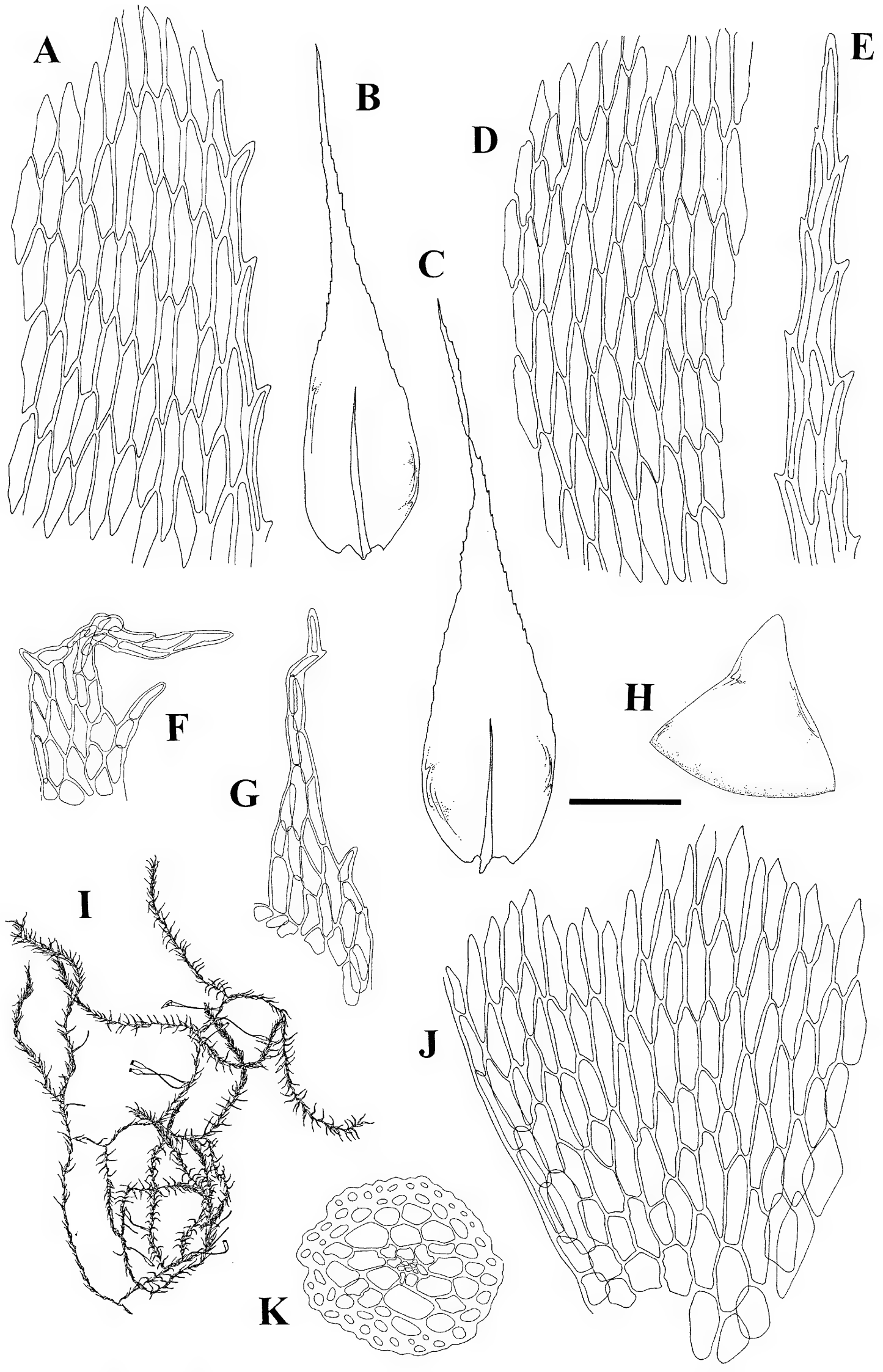


Figure 36. *Lindigia debilis*. A. Median leaf cells and margin. B & C. Leaves. D. Median leaf cells. E. Leaf apex. F & G. Pseudoparaphyllia. H. Operculum. I. Habit. J. Basal leaf cells. K. Stem in cross section. Scale in mm: bar = 0.06 (A, D, E, J); bar = 0.08 (F, G, K); bar = 0.34 (H); bar = 0.5 (B, C); bar = 1.3 (I). F, G, I from *Crosby 12590*; H from *Buck 9798*; all other figure parts from *Griffin 539*.

(1–4 mm long), papillose setae, broader exostome teeth that are horizontally striate dorsally at base, and broad, keeled, perforate endostomial segments.

5. *Meteoridium* (Müll. Hal.) Manuel, Lindbergia 4: 47. 1977. *Neckera* sect. *Pseudopilotrichum* Müll. Hal. subsect. *Meteoridium* Müll. Hal., Syn. Musc. Frond. 2: 672. 1851. *Pilotrichella* sect. *Meteoridium* (Müll. Hal.) Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 226. 1872. *Meteoriopsis* sect. *Meteoridium* (Müll. Hal.) Broth., Nat. Pflanzenfam. I(3): 825. 1906.

Meteoridium Müll. Hal., Linnaea 42: 492. 1879, invalid name, lacks a description or reference to previous description.

Plants very slender, medium-sized, or robust, in green, yellowish green, or golden brown, at times black tinged, dense, pendent masses. Primary stems creeping, secondary stems pendent, irregularly branched, not stipitate; stems in cross section with epidermal cells variously thickened, cortical cells enlarged, firm-walled, central strand weakly developed; paraphyllia absent; pseudoparaphyllia foliose; rhizoids in dense groups, dark brown to blackish, smooth, not branched, from clusters of initials abaxial to the leaf insertions. Stem leaves ovate-triangular, ovate-lanceolate, or lanceolate, abruptly long-acuminate to nearly piliferous, branch leaves ovate to narrowly lanceolate. All leaves distantly spaced, spreading from insertion or occasionally erect, somewhat contorted when dry, erect-spreading when wet, long-acuminate, apices nearly always twisted when wet or dry, inserted in a U-shaped line, cordate to reniform at base; margins plane or recurved at base, plane above, serrate to serrulate to near the leaf base, rarely entire; costae single, ending at midleaf, at times ending in a spine, in cross section cells homogeneous, thick-walled; cells smooth, upper and median cells linear to linear-fusiform, thick-walled, rarely porose; basal cells broader, usually porose; alar cells short-rectangular, thick-walled, porose, in small excavate groups. Asexual reproduction at times by deciduous flagelliform branches. Dioicous. Perichaetia lateral on stems and branches. Setae short, erect. Capsules erect, oblong to short-cylindric; exothecial cells at mouth subquadrate, red, lower cells rounded-rectangular, thick-walled, not collenchymatous; stomata phaneroporic, on neck; opercula obliquely short-rostrate; annuli rudimentary, persistent; peristome diplolepideous; exostome teeth reddish brown, narrowly triangular, cross-striate in lower half, papillose above; endostome yellowish, lightly papillose, basal membranes short, segments linear, keeled, perforate, cilia absent or rudimentary and reduced to low stubs. Spores round, lightly papillose. Calyptrae cucullate, smooth.

Meteoridium is a common and widely distributed Neotropical genus found from Mexico to Chile. When Manuel (1977c) revised the genus, *Meteoridium* was not known from the Amazon Basin. He attributed its absence to the incomplete knowledge of the bryoflora in that region, and indeed *Meteoridium* has since been found in the Amazonian parts of Ecuador (Churchill 1994), Colombia, and Peru (Churchill 1998). *Meteoridium* usually grows as an epiphyte, where it often occurs in long festoons on twigs, branches, or tree trunks. At lower elevations (below 1500 m) in Bolivia, however, it can be terrestrial on humus, loose sticks, rotten logs, boulders, and road cuts (Lewis 1992). Plants of *Meteoridium* are often tinged an intense black, and they have weakly differentiated, widely spaced stem and branch leaves that typically spread from the insertions. Its leaves commonly have twisted apices; margins nearly serrate throughout; and single costae that often end in a spine above midleaf. *Meteoridium* has smooth, linear leaf cells and poorly differentiated alar cells. It is a dioicous genus with shortly exserted, oblong to short-cylindrical capsules; exostome teeth cross-striate on the lower dorsal surface; and endostomial cilia that are absent or rudimentary. The calyptrae are smooth and cucullate.

Meteoridium is traditionally placed in the Meteoriaceae, close to, and sometimes merged with, *Zelometeorium*. That genus differs from *Meteoridium* in having stem and branch leaves more strongly differentiated; stem leaves clasping or sheathing the stems; calyptrae mitrate and hairy; and papillose exostome teeth. Support for placement of *Meteoridium* in the Meteoriaceae is present in its epiphytic habit; the ability of its gametophytes to produce an intense black color; short setae; erect, oblong capsules; and absent to rudimentary endostomial cilia. More recently, *Meteoridium* has been transferred to the Brachytheciaceae (Lewis 1992; Buck & Goffinet 2000). Evidence supporting the placement of *Meteoridium* in the Brachytheciaceae includes its tendency to sometimes occupy terrestrial habitats;

the close resemblance of many of its gametophytic features to those of *Rhynchostegium*; and the presence of cross-striations on the lower dorsal surface of the exostome teeth. At present, there is considerable uncertainty surrounding the circumscription of both the Meteoriaceae and Brachytheciaceae, *e.g.*, the morphological distinctions between the families in Buck and Goffinet (2000) are so slight that *Meteoridium* cannot be excluded from either family.

The name *Meteoridium* combines the generic name *Meteorium* with the Greek diminutive suffix *–idium*.

1. Plants rigid to loose, medium-sized to robust in dense, pendent masses; stem leaves broadly ovate-lanceolate to ovate-triangular, widely spaced, often overlapping; branch leaves 1–2 × 1.0 mm . . . . . 1. *M. remotifolium*
1. Plants soft, very slender, with filiform-flagelliform stems and branches; stem leaves ovate-lanceolate to lanceolate, distantly spaced, not overlapping; branch leaves 1.0–1.4 × 0.5 mm . . . . . 2. *M. tenuissimum*

1. *Meteoridium remotifolium* (Müll. Hal.) Manuel, Lindbergia 4: 49: 1977. *Leskea remotifolia* Müll. Hal., Linnaea 19: 216. 1846. *Neckera remotifolia* Hornsch. *ex* Müll. Hal., Linnaea 19: 216. 1846, invalid name, in synonymy. *Neckera remotifolia* (Müll. Hal.) Müll. Hal., Syn. Musc. Frond. 2: 672. 1851. *Meteorium remotifolium* (Müll. Hal.) Mitt., J. Linn. Soc., Bot. 12: 447. 1869. *Pilotrichella remotifolia* (Müll. Hal.) Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 226. 1872. *Meteoridium remotifolium* Müll. Hal., Linnaea 42: 492. 1879, invalid combination. *Meteoriopsis remotifolia* (Müll. Hal.) Broth., Nat. Pflanzenfam. I(3): 825. 1906. Protologue. Mexico. Prope Halapau-Ugornt. *Deppe & Schiede 1088*. Type (see Manuel 1977c). H, lectotype.

Plants medium-sized to robust, in green, yellowish or golden brown, often blackish tinged, dense, pendent masses. Primary stems creeping, secondary stems pendent, irregularly branched, not stipitate, to 40 cm long; stems in cross section with sclerodermis of 3–5 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, firm-walled, central strand weakly developed; paraphyllia absent; pseudoparaphyllia foliose; rhizoids in dense clusters, dark brown to blackish, smooth, not branched, from clusters of initials abaxial to the leaf insertions; axillary hairs 4–5 cells long, with 1–2 short, reddish brown, basal cells and 3 elongate, hyaline, upper cells. Stem and branch leaves differing only in shape, stem leaves ovate-triangular, abruptly long-acuminate to nearly piliferous, branch leaves ovate to lanceolate. Leaves 1–2 mm long, spreading from insertions (occasionally erect), somewhat contorted when dry, erect-spreading when wet, long-acuminate, apices nearly always twisted when wet or dry, inserted in a U-shaped line, cordate to reniform at base; margins plane, serrate to serrulate to near the leaf base, rarely entire; costae single, ending at midleaf, at times ending in a spine, in cross section cells homogeneous, thick-walled; cells smooth, upper and median cells linear to linear-fusiform, thick-walled, rarely porose, 50–90 × 5–7 µm; basal cells broader, usually porose; alar cells short-rectangular, thick-walled, porose, in small excavate groups. Asexual reproduction at times by deciduous flagelliform branches. Dioicous. Perichaetia lateral on stems and branches. Setae short, erect, red, smooth, 2–3 mm long. Capsules erect, oblong to short-cylindric, 1.5–2.0 mm long; exothecial cells short-rectangular, thick-walled, not collenchymatous; stomata on neck; opercula obliquely short-rostrate, 1.0 mm long; annuli rudimentary; peristome diplolepideous; exostome teeth reddish brown, narrowly triangular, cross-striate in lower half, papillose above; endostome yellowish, lightly papillose, basal membranes short, segments linear, keeled, perforate, cilia absent. Spores round, lightly papillose, 17–28 µm. Calyptrae cucullate, smooth, 2 mm long.

Illustrations. Bartram (1949, Fig. 121 E–G); Florschütz (1964, Fig. 104); Manuel (1977c, Fig. 2); Lewis (1992, Pls. 3, 5, 6 1–4); Sharp *et al.* (1994, Fig. 549); Churchill and Linares (1995, Fig. 122 e–i); Duarte Bello (1997, Pl. 195); Buck (1998, Pl. 99 1–9); Buck (2003, Fig. 123). Figure 37.

Habitat. Pendent from tree trunks and branches, slender shrubs, twigs, leaves, rotting logs, and palm fronds, occasionally on humus or soil; 75–2700 m.

Distribution in Central America. BELIZE. Toledo: *Allen 18681* (BRH, MO). GUATEMALA. Alta Verapaz: *Standley 89870* (F, FH, NY); Baja Verapaz: *Croat 41266A* (MO); Huehuetenango: *Steyermark 48769C* (F); Izabal: *Steyermark 39904D* (F); Quetzaltenango: *Standley 85011* (F, FH, NY);

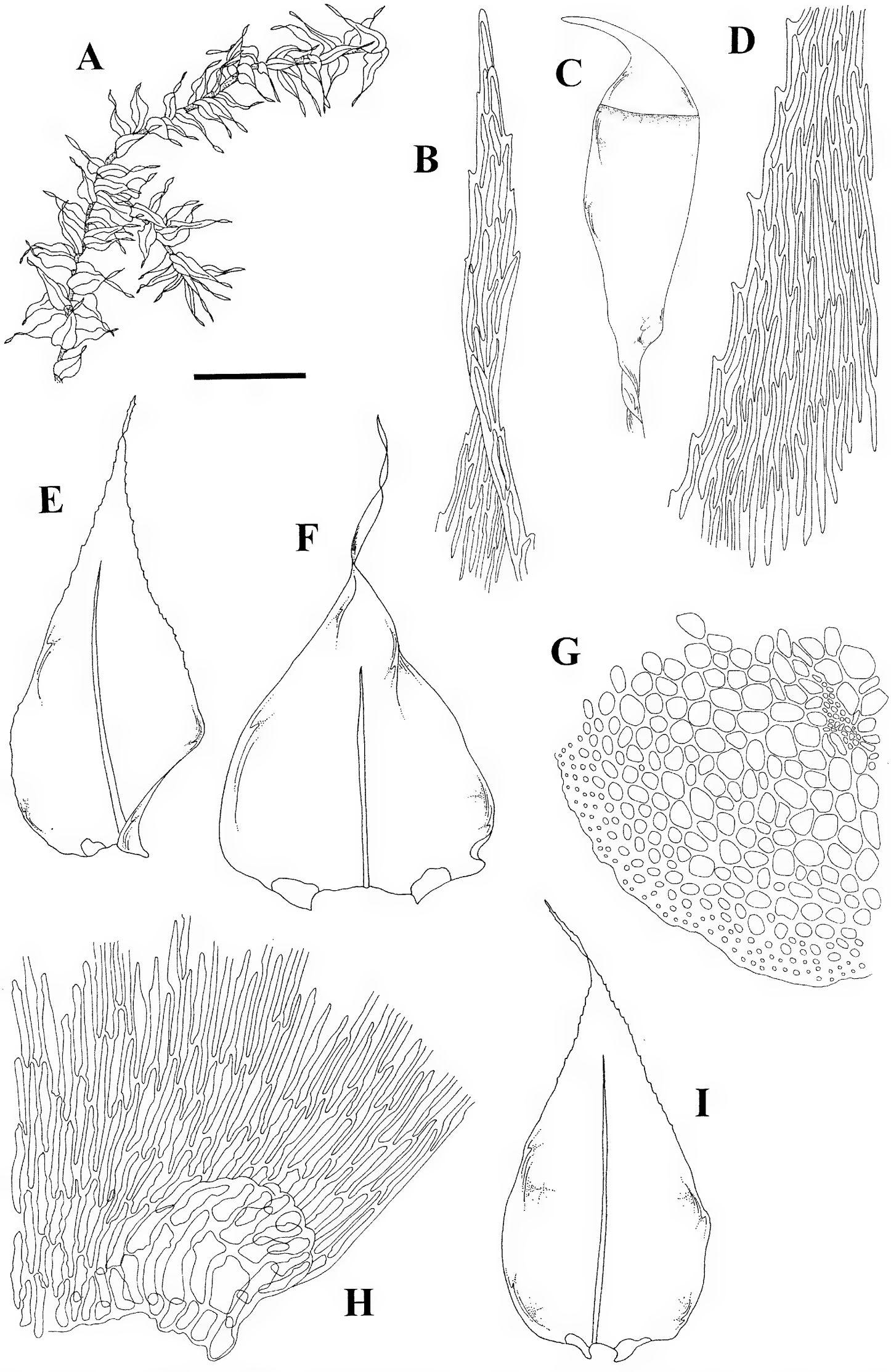
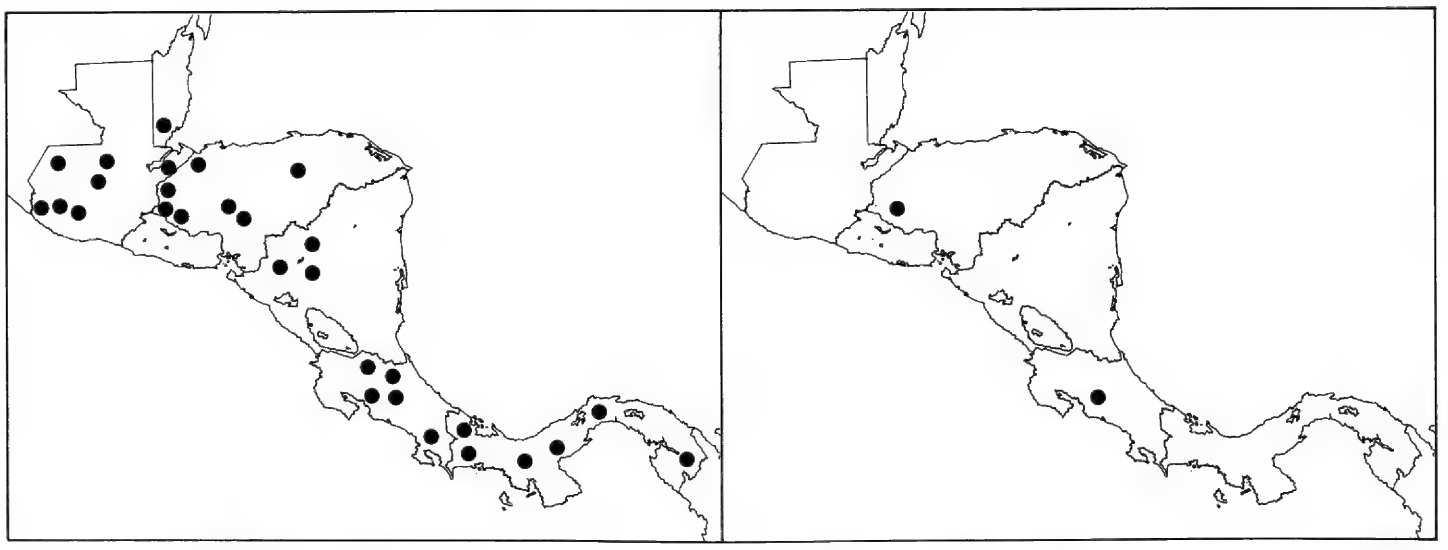


Figure 37. *Meteoridium remotifolium*. A. Habit. B. Leaf apex. C. Seta, capsule, and operculum. D. Median leaf cells and margin. E & I. Branch leaves. F. Stem leaf. G. Stem in cross section. H. Alar and basal leaf cells. Scale in mm: bar = 0.06 (B, D, H); bar = 0.08 (G); bar = 0.5 (E, F, I); bar = 0.8 (C); bar = 4 (A). C from *Crosby & Crosby 6486*; all other figure parts from *Allen 14375*.



Meteoridium remotifolium *Meteoridium tenuissimum*

San Marcos: *Croat 40814* (F, FH, GUAT, MO, NY, US); Sololá: *Steyermark 47951* (F, FH, MO, NY). HONDURAS. Comayagua: *Allen 13417* (MO); Copán: *Allen 17732* (MO, TEFH); Cortés: *Allen 14375* (MO, TEFH); Francisco Morazán: *Molina & Molina 27930* (F, MO); Lempira: *Allen 11360* (MO, TEFH); Ocotepeque: *Allen 14439* (MO, TEFH); Olancho: *Allen 12573* (MO, TEFH). NICARAGUA. Estelí: *Stevens & Montiel 16925* (HNMN, MO); Jinotega: *Croat 42937* (HNMN, MO); Matagalpa: *Richards et al. 3750* (F, FH, MO, NY). COSTA RICA. Alajuela: *Crosby & Crosby 6308* (MO); Cartago: *Crosby & Crosby 6085* (MO); Heredia: *Griffin et al. D230* (F, MO, NY); Puntarenas: *Davidse & Herrera 26214* (CR, MO); San José: *Croat 35285* (CR, F, FH, MO, NY, US). PANAMA. Bocas del Toro: *Allen 5257* (MO, PMA); Chiriquí: *Allen 5371* (MO, PMA); Coclé: *Crosby 4408* (F, MO, US); Darién: *Hammel et al. 16300* (MO); Panamá: *Crosby 4376* (MO); Veraguas: *Crosby 10819* (MO, PMA).

World range: Mexico; Central America; Caribbean; Western, Northern, and Southern South America, Brazil.

Meteoridium remotifolium is a common, medium-sized species that is usually pendent from twigs and branches. Although in Central America the species sometimes occurs terrestrially on road banks or in the forests, these plants appear to be epiphytes that have persisted after falling to the ground. *Meteoridium remotifolium* has widely spaced stem and branch leaves that spread from a U-shaped insertion. The leaves have sharply serrate margins; weak, single costae that occasionally end with a spine just above midleaf; and narrowly acuminate to piliferous, consistently twisted apices. Its upper and median leaf cells are smooth and linear, the basal cells are typically porose, and the alar cells are differentiated in small, excavate groups of short-rectangular, porose cells. *Meteoridium tenuissimum* differs from *M. remotifolium* in its much smaller size and more widely spaced, ovate-lanceolate to lanceolate stem leaves. The differences between the two species are mostly quantitative. Lewis (1992), for example, considered the branch tip leaves of *M. remotifolium* indistinguishable from the leaves of *M. tenuissimum*.

Zelometeorium patulum and *Meteoridium remotifolium* are often confused. That species differs from *M. remotifolium* in having clasping stem leaves, squarrose-spreading branch leaves that are strongly differentiated from the stem leaves, mitrate calyptrae, and exostome teeth that are papillose throughout. Members of the genus *Rhynchostegium* and *M. remotifolium* have very similar gametophytes, but *Rhynchostegium* is a more consistently terrestrial genus with plants that are never blackish tinged and have broadly acuminate leaf apices. Its sporophytes differ from those of *M. remotifolium* in having elongate setae, asymmetric capsules, and well-developed cilia.

2. *Meteoridium tenuissimum* (Hook. & Wilson *in* Wilson) M. A. Lewis, Trop. Bryol. 5: 41: 1992. *Cryphaea tenuissima* Hook. & Wilson *in* Wilson, London J. Bot. 5: 453. 1846. *Pilotrichella tenuissima* (Hook. & Wilson *in* Wilson) Hampe, Flora 45: 455. 1862. *Meteorium tenuissimum* (Hook. & Wilson *in* Wilson) Mitt., J. Linn. Soc., Bot. 12: 447. 1869. *Floribundaria tenuis-*

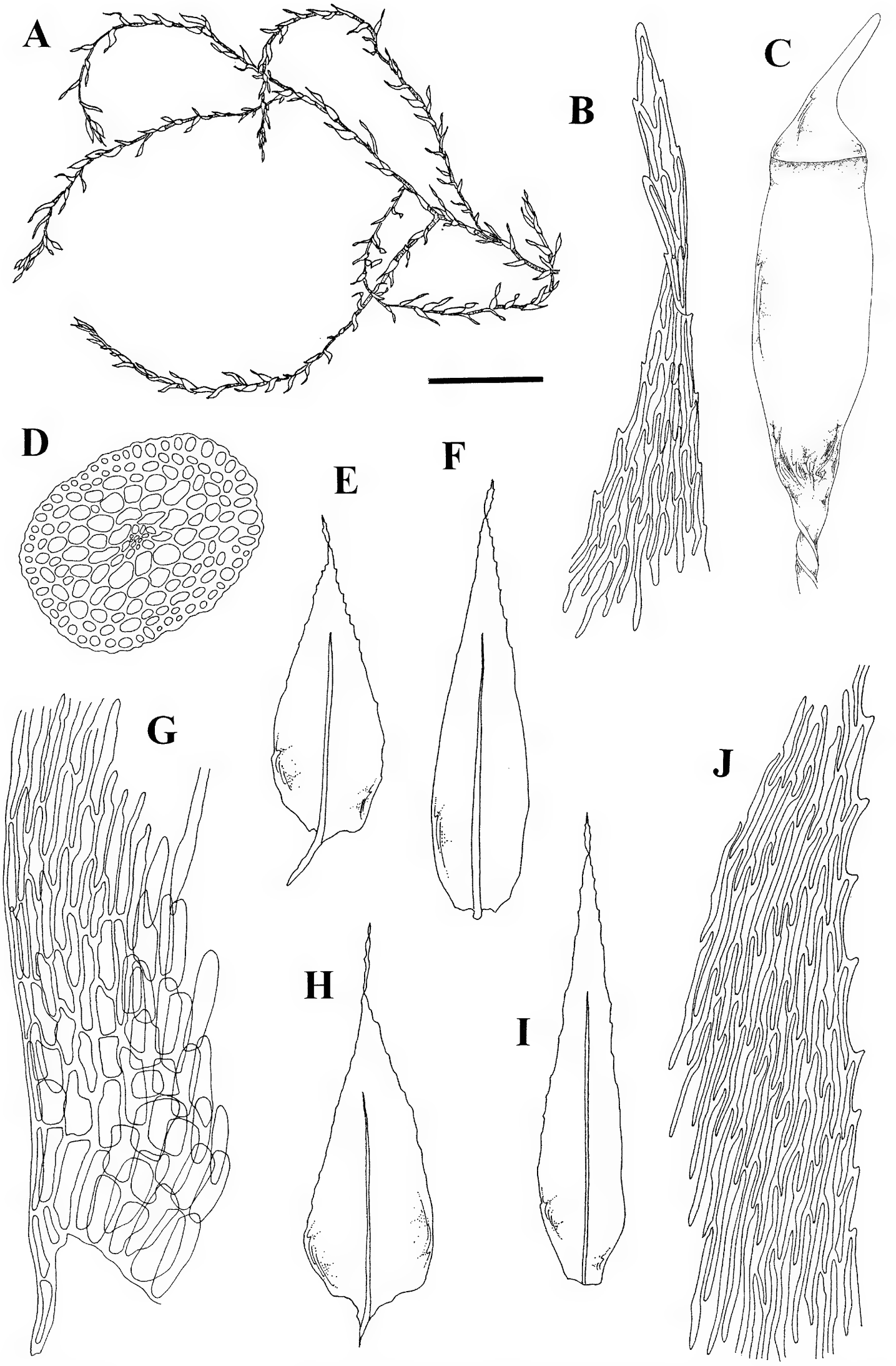


Figure 38. *Meteoridium tenuissimum*. A. Habit. B. Leaf apex. C. Seta, capsule, and operculum. D. Stem in cross section. E, F, H & I. Leaves. G. Alar and basal leaf cells. J. Median leaf cells and margin. Scale in mm: bar = 0.05 (B, G, J); bar = 0.06 (D); bar = 0.41 (E, F, H, I); bar = 0.8 (C); bar = 3.3 (A). C from *Hegewald & Hegewald 8703*; D from *Churchill 22418*; F & I from *Van der Werff 9607*; all other figure parts from *Liesner 13041*.

sima (Hook. & Wilson *in* Wilson) Broth., Nat. Pflanzenfam. I(3): 821. 1906. *Barbella tenuissima* (Hook. & Wilson *in* Wilson) M. Fleisch. *in* Broth., Nat. Pflanzenfam. (ed. 2) 11: 169. 1925. Protologue. Ecuador. Woods, Baños, *Jameson*.

Plants very slender, soft, in yellowish green, filiform-flagelliform, festooning masses. Primary stems and branches elongate, irregularly branched, not stipitate, to 40 cm long; stems in cross section with 1–2 rows of somewhat enlarged, firm-walled epidermal cells, cortical cells enlarged, yellow, firm-walled, central strand weakly developed; paraphyllia absent; pseudoparaphyllia foliose; rhizoids sparse, in dense clusters, dark brown to blackish, smooth, not branched, from elongate clusters of initials abaxial to the leaf insertions; axillary hairs with 1 short, reddish brown, basal cell and 1–2 elongate, hyaline, upper cells. Primary stem leaves ovate-lanceolate to lanceolate; branch leaves lanceolate to narrowly lanceolate, 0.9–1.6 × 0.3–0.5 mm. Leaves distantly spaced, not or rarely touching the leaf above, usually spreading from insertions, erect-spreading when dry, long-acuminate, apices often twisted when wet or dry, inserted in a shallow U-shaped line; margins recurved at base, plane above, serrate to serrulate to near the leaf base; costae single, ending above midleaf, at times ending in a spine, in cross section cells homogeneous, thick-walled; cells smooth, median cells linear to linear-fusiform, thick-walled, rarely porose, 60–90 × 4–5 µm; alar cells in small groups of short-rectangular to subquadrate, thick-walled, porose cells. Dioicous. Perichaetia lateral on stems and branches. Sporophytes unknown in Central America, description from Peru (*Bryophyta Neotropica 2*, MO). Setae short, straight, red, smooth, 3–4 mm long, twisted when dry. Capsules erect, oblong to short-cylindric, 2–3 mm long; exothecial cells at mouth subquadrate, red, lower cells rounded-rectangular, thick-walled, not collenchymatous; stomata phaneroporic, on neck; opercula obliquely short-rostrate, 1.0 mm long; annuli rudimentary, persistent; peristome diplolepideous; exostome teeth reddish brown, narrowly triangular, cross-striate in lower half, papillose above; endostome yellowish, lightly papillose, basal membranes low to medium-high, segments linear, keeled, perforate, cilia absent or rudimentary and reduced to low stubs. Spores round, lightly papillose, 20–32 µm. Calyptrae cucullate, naked, 1–2 mm long.

Illustrations. Wilson (1846, Pl. 15 E); Lewis (1992, Pls. 4, 6 5–10); Churchill and Linares (1995, Fig. 123 a–e). Figure 38.

Habitat. Festooning tree and shrub trunks, branches, and twigs; 1500–2100 m.

Distribution in Central America. HONDURAS. Lempira: *Allen 11932* (MO). COSTA RICA. San José: *Valerio 309* (FH, US).

World range: Central America; Western and Northern South America.

Plants of *Meteoridium tenuissimum* are remarkably soft and slender, with wide-spreading leaves that are so well spaced they rarely touch. Its leaves have strong, single costae that end above midleaf, occasionally in a spine; serrate to serrulate margins; and weakly developed alar cells. Plants of *M. tenuissimum* are remarkably similar to those of *M. remotifolium* in gametophytic as well as sporophytic features. The gametophytes of *M. remotifolium* are stiffer than those of *M. tenuissimum*, and they are typically larger in all aspects. Although both species have wide-spreading, well-spaced leaves, the leaves of *M. remotifolium* are closer together than those of *M. tenuissimum* and contiguous leaves normally overlap. Well-developed plants of *M. remotifolium* also differ from those of *M. tenuissimum* in having broadly ovate-lanceolate to ovate-triangular rather than ovate-lanceolate to lanceolate stem leaves. Lewis (1992), however, considered the ultimate branch leaves of *M. remotifolium* indistinguishable from the leaves of *M. tenuissimum*. The close gametophytic similarity between these two species makes small or depauperate collections of *M. remotifolium* very difficult to separate from *M. tenuissimum*. Although the sporophytes of *M. tenuissimum* and *M. remotifolium* are structurally identical, curiously the sporophytes of *M. tenuissimum* are larger in all aspects than those of *M. remotifolium*.

Aptychella proligera (Broth.) Herzog sometimes grows mixed (see *Holz & Schäfer-Verwimp CR 99-1131*, MO) with *M. tenuissimum*, and both species have the same size, soft, slender aspect, and widely spaced leaves. Plants of *A. proligera* differ from those of *M. tenuissimum* in having narrower leaves; subentire to serrulate upper leaf margins; short, double costae; and thick-walled, somewhat

enlarged alar cells. *Aptychella proligera* can be distinguished macroscopically from *M. tenuissimum* by its deep red colored stems and clusters of red propagula at the ends of the primary branches.

6. *Meteorium* (Brid.) Dozy & Molk., Musci Frond. Ined. Archip. Ind. 157. 1848. *Pilotrichum* [subgen.] *Meteorium* Brid., Bryol. Univ. 2: 264. 1827.

Neckera Hedw. sect. *Pseudopilotrichum* Müll. Hal. subsect. *Papillaria* Müll. Hal., Syn. Musc. Frond. 2: 134. 1850. *Papillaria* (Müll. Hal.) Lorentz, Moosstudien 165. 1864. *Pilotrichella* sect. *Papillaria* (Müll. Hal.) Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 227. 1872. *Meteorium* sect. *Papillaria* (Müll. Hal.) Mitt., J. Linn. Soc., Bot. 22: 314. 1886.
Monoschisma Duby, Mém. Soc. Phys. Hist. Nat. Genève 19: 294. 1867.
Tricholepis Kindb., Bot. Centralbl. 77: 52. 1899.

Plants slender, medium-sized to robust, in dull green, yellow green, or golden red, at times jet black tinged, soft or stiff tufts, mats, or pendent masses. Stems creeping, horizontal, erect, or pendent, irregularly to pinnately branched, not stipitate; stems in cross section with sclerodermis of small, yellow or red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, firm-walled, central strand weakly developed; paraphyllia absent; pseudoparaphyllia foliose, cells smooth or papillose; rhizoids sparsely developed, reddish brown, smooth, not branched, from dense, circular clusters of initials abaxial to the leaf insertions; axillary hairs with 1–2 short, brown, basal cells and 2–4 short, rounded, hyaline, upper cells. Stem leaves ovate-triangular, oblong-obovate, or lanceolate, variously concave, at times cucullate, clasping and variously cordate at base, margins often wavy or undulate. Branch leaves oblong-ovate, ovate, or ovate-triangular, occasionally lanceolate. Leaves erect to erect-appressed or imbricate when dry, erect to somewhat spreading when wet, apiculate, short- to long-acuminate, or tapered to hair-points, concave, plicate or smooth, cordate and clasping at base, decurrent; margins plane, erect or incurved, crenulate by projecting papillae, at times sharply serrate at base; costae single, ending at or a little above midleaf, in cross section with superficial guide cells somewhat enlarged, other cells homogeneous and thick-walled; cells unipapillose or pluripapillose, papillae seriate or scattered over the cell lumina and cell walls; upper cells oval, rhombic, fusiform, or linear, firm-walled, median cells linear; basal cells oblong to rectangular, often smooth and porose, cells in cordate base elongate or rhombic to fusiform; alar cells subquadrate, smooth, firm-walled, often porose in small area above decurrencies. Asexual reproduction at times by deciduous, flagelliform branches or attenuate branch tips with caducous leaves. Dioicous. Vaginulae densely hairy. Setae long, roughened to scabrous throughout. Capsules erect, elliptic, oblong, or short-cylindric; exothecial cells oblate in 3–5 rows at mouth, lower cells short-rectangular to subquadrate, firm-walled, not collenchymatous; stomata superficial on neck; opercula obliquely long-rostrate or conic-rostrate; annuli rudimentary, of quadrate, thick-walled cells; peristome diplolepideous, yellowish white or reddish yellow; exostome teeth narrowly triangular, papillose throughout, median line thickened; endostome papillose, basal membranes low, segments linear, not perforate, cilia absent or rudimentary. Spores irregularly rounded, lightly papillose. Calyptrae cucullate, densely hairy.

Meteorium is a genus of about 36 species found mostly in the tropical regions of the world. As treated here, *Meteorium* includes *Papillaria*, which considerably expands the size of the genus. *Papillaria* differs from *Meteorium* only in having consistently pluripapillose leaf cells. In *Meteorium s. str.* the leaf cells are predominantly unipapillose, but in most collections a few cells with 2–3 papillae can usually be found.

Plants of *Meteorium* have wide ecological amplitude. They occur as epiphytes in dense, often pendent masses or at the base of trees, as well as terrestrially on soil banks and over rocks. At times the plants have an intense blackish color. Typically, the genus has a creeping habit with stem and branch leaves that can be weakly or distinctly differentiated. The leaves are mostly erect when dry; rarely have twisted apices; at times are strongly clasping at base; have mostly crenulate-papillose margins; and have single costae that end above midleaf. The upper leaf cells in *Meteorium* are generally elongate, uni- or pluripapillose, and the alar cells are poorly differentiated. *Meteorium* is dioicous and sporophytes are not often encountered. It has elongate, roughened setae, oblong to short-cylindrical capsules, obliquely rostrate opercula, and densely hairy, cucullate calyptrae. Its peristome

is reduced, often pale in color, with narrow, papillose exostome teeth; the endostome has a low basal membrane, narrow segments, and rudimentary cilia.

The name *Meteorium* comes from the Greek *meteoros* (high in the air, suspended, raised, pertaining to things or phenomena in the air), and this apparently refers to the often pendent habit of the genus.

1. Leaves oblong, deeply concave and cucullate above; branch leaf apices, especially those in the apical buds, apiculate . . . . . 4. *M. teres*
1. Leaves ovate-triangular, lanceolate, or oblong-ovate, plane or weakly concave above; branch leaf apices short- to long-acuminate or hair-pointed. 2

2. Leaves smoothly imbricate when dry; cells densely verruculose-papillose with papillae scattered over the lumina and cell walls . . . . . 2. *M. laevifolium*
2. Leaves erect to erect-appressed when dry; cells with 1–6 papillae centered over the lumina. 3

3. Leaves short- to long-acuminate or short hair-pointed, rarely with colorless, capillary hair-points; cells in cordate base short, mostly 2:1; plants often with deciduous leaves . . . . . 3. *M. nigrescens*
3. Leaves, especially those in the apical buds, with colorless, capillary hair-points; cells in cordate base elongate to linear; plants without deciduous leaves . . . . . 1. *M. deppei*

1. *Meteorium deppei* (Hornsch. *ex* Müll. Hal.) Mitt., J. Linn. Soc., Bot. 12: 441. 1869. *Neckera deppei* Hornsch. *ex* Müll. Hal., Syn. Musc. Frond. 2: 136. 1850. *Pilotrichella deppei* (Hornsch. *ex* Müll. Hal.) Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 224. 1872. *Papillaria deppei* (Hornsch. *ex* Müll. Hal.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 264. 1877. Protologue. Mexico: *Deppe et Schiede* pr. Xalapam legerunt.

Anomodon flexilis Hampe, Linnaea 12: 350. 1838. *Pilotrichum flexile* (Hampe) Hampe *ex* Müll. Hal., Syn. Musc. Frond. 2: 138. 1850. *Leskea flexilis* (Hampe) Hornsch. *ex* Müll. Hal., Syn. Musc. Frond. 2: 138. 1850, illegitimate homonym, not *Leskea flexilis* Hedw., Sp. Musc. Frond. 234. 1801. *Papillaria flexilis* (Hampe) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 268. 1877. *Meteorium flexile* (Hampe) Spessard, Mongr. Gen. *Meteorium* Mexico 108. 1980, combination illegitimate, published in a thesis, and illegitimate homonym, not *Meteorium flexile* (Hedw.) Mitt., J. Linn. Soc., Bot. 12: 438. 1869. Protologue. Ad arbores Mexicanos pendulus, *sin. coll.*

Antitricha cuspidata Nees, Linnaea 19: 681. 1847. Not *Meteorium cuspidatum* Okamura, Bot. Mag. (Tokyo) 25: 143. 1911. Protologue. In Mexico loco non citato leg. *Aschenborn*.

Neckera sinuata Müll. Hal., Syn. Musc. Frond. 2: 139. 1850. *Pilotrichum sinuatum* (Müll. Hal.) Hampe, Linnaea 25: 362. 1853. *Meteorium sinuatum* (Müll. Hal.) Mitt., J. Linn. Soc., Bot. 12: 446. 1869. *Pilotrichella sinuata* (Müll. Hal.) Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 226. 1872. *Papillaria sinuata* (Müll. Hal.) Paris, Index Bryol. 909. 1896. Protologue. Mexico, inter *Neckeram cochlearifoliam* crescens: *C. Ehrenberg* sterilem legit.

Meteorium illecebrum Sull., Proc. Amer. Acad. Arts 5: 285. 1861. *Neckera illecebra* Müll. Hal., Syn. Musc. Frond. 2: 137. 1850, illegitimate name, includes *Antitricha cuspidata* Nees and *Anomodon flexilis* Hampe in synonymy. *Pilotrichella illecebra* (Sull.) Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 225. 1872. *Papillaria illecebra* (Sull.) Broth., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 21, Afd. 3(3): 47. 1895. *Papillaria illecebra* (Sull.) Paris, Index Bryol. 905. 1896, superfluous combination. *Pilotrichum illecebrum* (Sull.) Hampe *ex* Paris, Index Bryol. 905. 1896, invalid name, listed in synonymy. Protologue. [Cuba] On high mountains [*Wright*] *84*.

Monoschisma viride Duby, Mém. Soc. Phys. Hist. Nat. Genève 19: 294. 1868. *Neckera dubyana* Hampe, new name, not *Neckera viridis* Müll. Hal., Syn. Musc. Frond. 2: 125. 1850. *Pilotrichella dubyana* (Hampe) Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 224. 1872, illegitimate combination, the epithet *viridis* was available in *Pilotrichella*. *Papillaria dubyana* (Hampe) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 264. 1877, illegitimate combination, the epithet *viridis* was available in *Papillaria*. Protologue. Ad truncos arborum in terris calidis Mexicanis reperiit *D. Sumichrast*.

Pilotrichella fusco-viridis Hampe, Flora 45: 455. 1862, invalid name, lacks a description. Protologue. Colombia. Bogota, 2700 Mtrs., [*Lindig*]. Base on: Herb Lindig, Nova Granata, Bogota ad ramos. Alt. 2700 metr., 1860 Nov. (US).

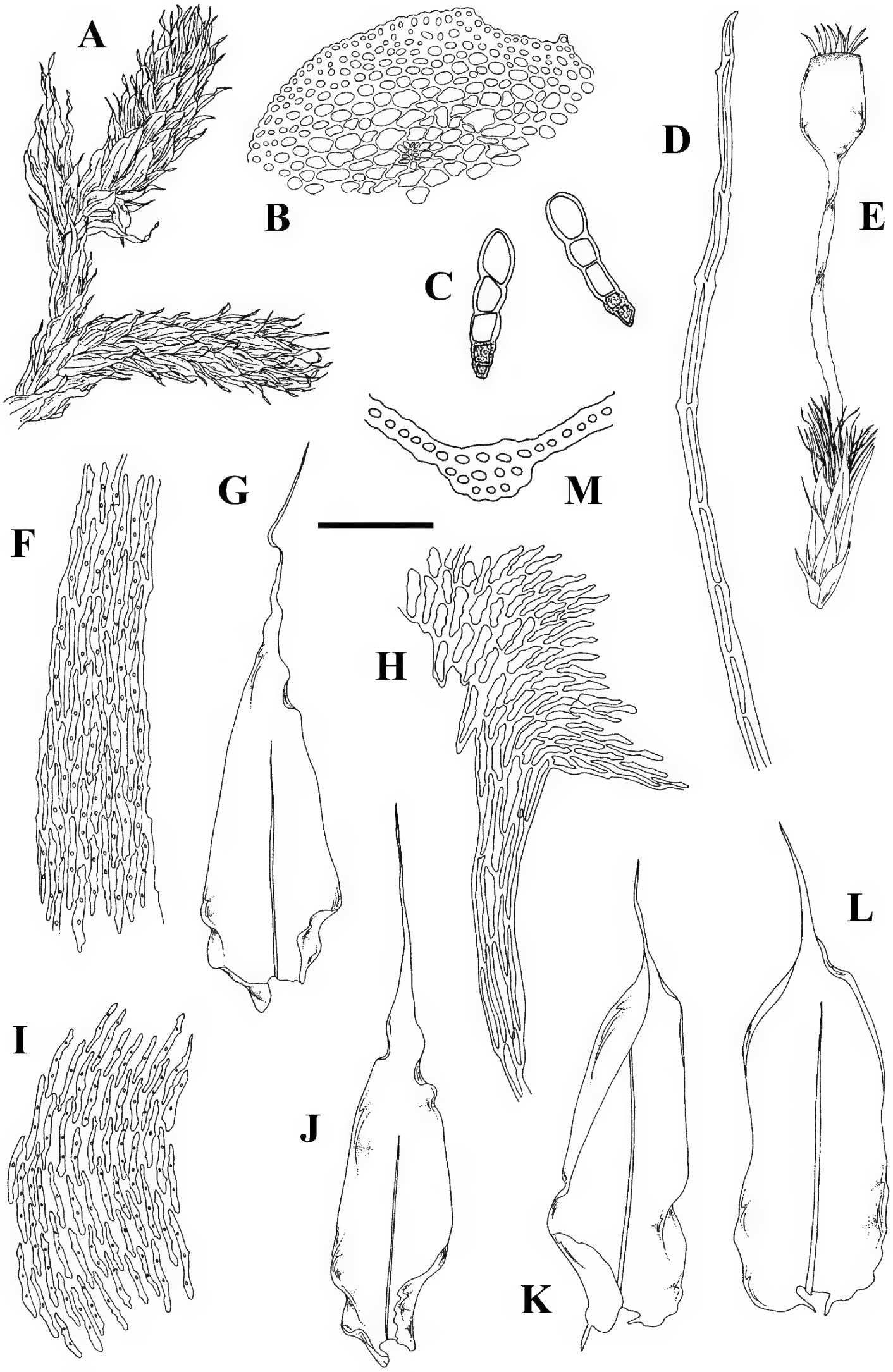
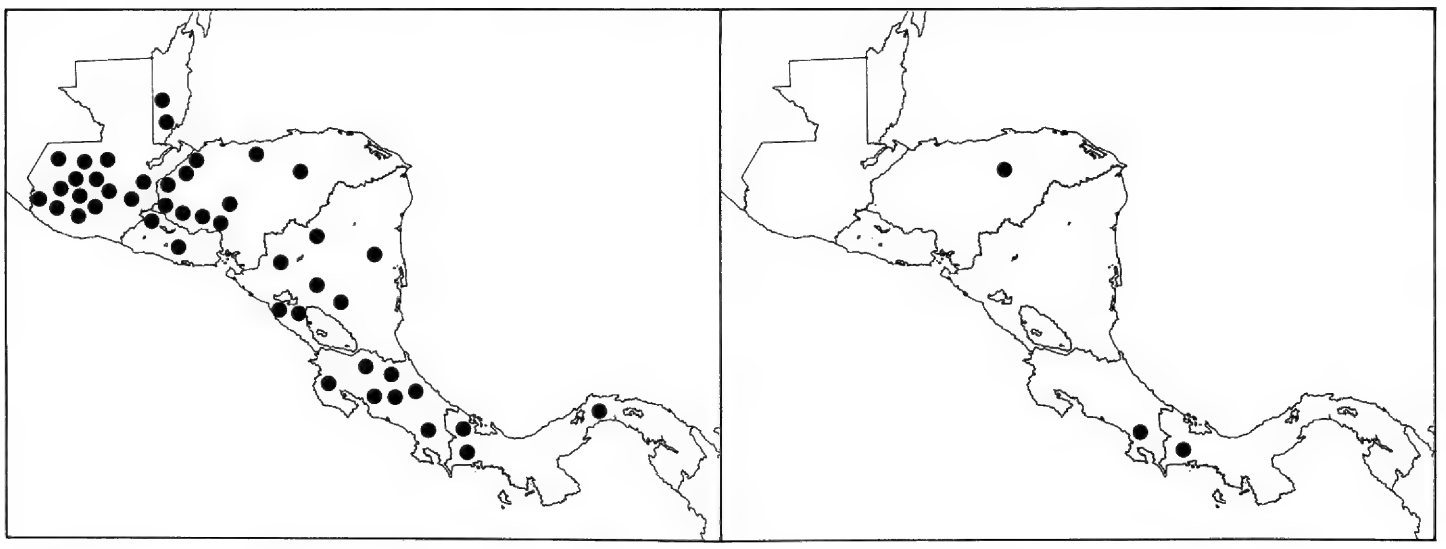


Figure 39. *Meteorium deppei*. A. Habit. B. Stem in cross section. C. Axillary hairs. D. Leaf hair-point. E. Sporophyte. F. Median leaf cells and margin. G & J. Stem leaves. H. Leaf alar region and decurrency. I. Median leaf cells. K & L. Branch leaves. M. Costa in cross section. Scale in mm: bar = 0.04 (C, M); bar = 0.05 (B); bar = 0.06 (D, F, H, I); bar = 0.9 (G, J, K, L); bar = 1.66 (E); bar = 4 (A). E from *Allen 11970*; all other figure parts from *Allen 14480*.



Meteorium deppei *Meteorium laevifolium*

Neckera fusco-viridis Hampe, Linnaea 31: 526. 1862. *Papillaria fusco-viridis* (Hampe) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 269. 1877. Protologue. [Colombia] Nova-Granada, Cipacon cum priore [*Lindig*].

Meteorium undulifolium Broth. & Thér., Recueil. Publ. Soc. Havraise Études Diverses 88: 311. 1921. Protologue. [Costa Rica] La Palma, près San José, alt. 1500 m (*C. Wercklé*, avril 1910). Type. Costa Rica, La Palma, près San José, 1500 m, leg. *C. Wercklé*, avril 1910, no. 15, *syn. nov.* (H).

Meteorium illecebrum Sull. var. *gracile* Cardot *ex* Thér., Rev. Bryol. Lichénol. 5: 105. 1932 [1933] [“*gracilis*”]. Protologue. Mexico. Pringle Pl. mexic *n*^{o} *10607*. Types. State of Mexico. Amecameca, 8500 ft., 11, Sept., 1908, [*Pringle*] *10607* (MO, US, isotypes).

Meteorium pseudoteres W. R. Buck, Mem. New York Bot. Gard. 82: 268. 1998. Protologue. Jamaica. John Crow Peak, 5800–6000 ft., on trees, 2 Feb. 1903, *L. M. Underwood 714*. Types. Jamaica. On trees. John Crow Peak (upper altitudes 5800–6000 ft.), *L. M. Underwood No. 714*, 2 February 1903 (NY, holotype; NY, isotype), *syn. nov*.

Plants medium-sized to robust, in dull green, yellow green, jet black tinged tufts, mats, or pendent masses. Stems creeping, horizontal, erect, or pendent, irregularly to pinnately branched, not stipitate, to 25 cm long; stems in cross section with sclerodermis of 2–5 rows of small, yellow or red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, firm-walled, central strand weakly developed; paraphyllia absent; pseudoparaphyllia foliose, cells papillose; rhizoids sparsely developed, reddish brown, smooth, not branched, from dense circular clusters of initials abaxial to the leaf insertions; axillary hairs with 1–2 short, brown, basal cells and 3–4 short, rounded, hyaline, upper cells. Stem leaves variable in shape, but typically lanceolate with wavy upper margins, clasping and cordate at base. Branch leaves variable in shape but typically oblong-ovate. Leaves erect to erect-appressed when dry, erect to somewhat spreading when wet, 1.6–4.0 mm long, gradually or abruptly tapered to long, slender hair-points, concave, varying from strongly plicate to smooth, cordate at base, decurrent; margins plane, erect or incurved above, crenulate by projecting papillae; costae single, ending at or a little above midleaf, in cross section cells with superficial guide cells somewhat enlarged, other cells homogeneous and thick-walled; cells unipapillose or pluripapillose with 1–6 papillae scattered over the cell lumina, upper cells fusiform to linear, firm-walled, 15–60 × 4–7 µm; median cells linear, 24–67 µm; basal cells oblong to rectangular, 17–45 × 5–11 µm, often smooth and porose, cells in cordate base elongate; alar cells weakly developed, subquadrate, smooth, firm-walled, often porose. Asexual reproduction at times by microphyllous flagellate branches, leaves not caducous. Dioicous. Vaginulae densely hairy. Setae long, flexuose, yellow or yellowish brown, roughened to scabrous throughout, 4–10 mm long. Capsules erect, elliptic to short-cylindric, 1.5–2.3 mm long; exothecial cells oblate in 3–5 rows at mouth, lower cells short-rectangular to subquadrate, firm-walled, not collenchymatous; stomata superficial on neck; opercula obliquely long-rostrate, 0.8–1.4 mm long; annuli rudimentary, of quadrate, thick-walled cells; peristome diplolepideous, yellowish white; exostome teeth narrowly triangular, papillose throughout, median line thickened; endostome papillose, basal membranes low, segments linear, not perforate, cilia absent or rudimentary. Spores irregularly rounded, lightly papillose, 14–30 µm. Calyptrae cucullate, densely hairy, 2–3 mm long.

Illustrations. Duby (1868, Fig. 1); Thériot (1921, Fig. 4, as *Meteorium undulifolium*); Bartram (1949, Fig. 119 F–G, as *Papillaria deppei*; Fig. 120 A–C, as *Meteorium illecebrum*); Spessard (1980, Figs. 14, 16, as *Meteorium flexilis*); Sharp *et al.* (1994, Fig. 544, as *Papillaria deppei*; Fig. 545 f–i, as *Meteorium illecebrum*); Churchill and Linares (1995, Fig. 123 f–h); Duarte Bello (1997, Pl. 196, as *Meteorium dubyanum*; Pl. 197, as *Meteorium illecebrum*; Pl. 198, as *Papillaria deppei*); Buck (1998, Pl. 103 1–9). Figure 39.

Habitat. On tree and shrub trunks, branches, vines, and twigs, often pendent and in the canopy, on leaves, palm fronds, rotting logs, soil banks, and rocks; 200–3400 m.

Distribution in Central America. BELIZE. Cayo: *Allen 18389* (BRH, MO); Toledo: *Allen 18640* (BRH, MO). GUATEMALA. Alta Verapaz: *Croat 41584B* (GUAT, MO, NY); Baja Verapaz: *Croat 41265* (FH, GUAT, MO); Chimaltenango: *Standley 57938* (F, FH, US); El Progreso: *Steyermark 43485a* (F, FH); Guatemala: *Standley 58412b* (F, FH); Huehuetenango: *Standley 83037* (F, FH, NY, US); Jalapa: *Standley 77500* (F, FH); Quetzaltenango: *Standley 66389* (F, FH); Quiché: *Hermann 26367a* (US); Sacatepéquez: *Standley 58873a* (F, FH); San Marcos: *Steyermark 35681* (F, FH, NY); Sololá: *Kellerman s.n.* (US); Totonicapán: *Standley 84038* (F, FH, NY); Zacapa: *Steyermark 43149* (F, FH, MO, NY, US). EL SALVADOR. Chalatenango: *Sipman et al. 37665* (MO, NY); Santa Ana: *Watson ES-0119* (MO); San Vicente: *Lagos & Montalvo 68* (MO). HONDURAS. Atlántida: *Allen 17480* (MO, TEFH); Comayagua: *Allen 13702* (MO, TEFH); Copán: *Allen 17754* (MO, TEFH); Cortés: *Allen 14177* (MO, TEFH); Intibucá: *Standley 25185* (F); La Paz: *Allen 14548* (MO); Lempira: *Allen 11393* (MO, TEFH); Ocotepeque: *Allen 14480* (MO, TEFH); Olancho: *Allen 12475* (MO, TEFH); Santa Bárbara: *Allen 11652A* (MO, TEFH). NICARAGUA. Chontales: *Stevens 22594* (MO); Estelí: *Moreno 11125D* (MO); Granada: *Baker 2525* (MO); Jinotega: *Stevens 11623* (HNMN, MO); Managua: *Standley 8150* (F); Matagalpa: *Croat 43142* (MO); Zelaya: *Stevens 7536* (MO). COSTA RICA. Alajuela: *McQueen 5051* (MO); Cartago: *Croat 47090A* (CR, MO, NY, US); Guanacaste: *Dauphin & Valdelomar 2481* (MO); Heredia: *Crosby & Crosby 6489* (MO); Limón: *Standley & Valerio 48353* (FH, US); Puntarenas: *Bowers 708* (MO); San José: *Griffin & Morales C144* (F, MO). PANAMA. Bocas del Toro: *Allen 5269* (MO); Chiriquí: *Croat 26288* (MO, PMA, NY, US); Panamá: *Crosby 10096* (MO).

World range: Mexico; Central America; Caribbean; Western, Northern, and Southern South America, Brazil.

Meteorium deppei is a common moss in Central America, where it grows principally as an epiphyte. The species has decurrent, hyaline hair-pointed leaves with elongate, uni- or pluripapillose leaf cells, and poorly developed alar cells. Outside of these few features the gametophytes of *M. deppei* are incredibly variable. When growing pendent on tree branches and twigs the species has a small, slender aspect. This form of the species (the type concept of *M. deppei*) has smooth, consistently long, hair-pointed stem and branch leaves that are erect and strongly clasping at base, and have basal leaf margins that are strongly and consistently recurved when dry. The form also has consistently pluripapillose leaf cells. When the plants grow on rocks or soil banks they are robust and often turgid in aspect. This form of the species (the type concept of *M. illecebrum*) has strongly plicate leaves with short hair-points, weakly or not clasping leaf bases, basal leaf margins that are never recurved when dry, and mostly unipapillose leaf cells. These two forms of the species are so different that without the benefit of examining many collections it is hard to accept them as variations of the same species. However, there are numerous collections with intermediate character states that cannot be assigned to either of the two extreme expressions. Individual plants are also extremely plastic, and at times some parts of single collections resemble the *deppei*-form, while other parts of the same collections resemble the *illecebrum*-form. This broad species view of *M. deppei* has been discussed by Crum and Steere (1957), Florschütz (1964), and Buck (1998).

Throughout its range there are robust, turgid collections of *M. deppei* that have entirely or mostly smooth rather than plicate leaves. This form, described as *Meteorium pseudoteres* (Buck 1998), has the macroscopic aspect of *Squamidium leucotrichum*, and further differs from typical expressions of *M. deppei* in having weakly decurrent leaves with incurved upper leaf margins, cordate-auriculate bases, and very poorly developed alar cells. Taken together this suite of features seems to well delineate the form, but every one of the features occurs in more typical collections of *M. deppei*. Further-

more, some branches with plicate leaves can nearly always be found in collections otherwise having smooth leaves, while plants with auriculate-cordate leaf bases are common in the *deppei*-form of the species. Incurved leaf margins are not a consistent feature of even *M. pseudoteres* (see Pl. 103, figs. 12 & 17, Buck 1998), and alar cell development within *M. deppei* is too variable, including within leaves from the same collection, to be any use in circumscribing *M. pseudoteres.*

Meteorium nigrescens and *M. deppei* are similar in having the same range of gametophytic variability. In general, *M. nigrescens* is a smaller plant than *M. deppei* and its leaves have shorter hair-points. However, there are forms of *M. nigrescens* with leaves as long hair-pointed as those of *M. deppei*, and some slender forms of *M. deppei* have the same size as *M. nigrescens*. The two species can be consistently distinguished by examining the cells in their cordate leaf bases. In *M. nigrescens* these cells are short, more or less 2:1 (length vs. width), while the cells in *M. deppei* are elongate to linear.

Floribundaria flaccida can be very difficult to distinguish from the slender forms of *Meteorium deppei*, since both species have long, hyaline hair-pointed leaves that are similar in shape, as well as areolation. The leaves of *F. flaccida*, however, are well spaced along the stems, and they spread from the base rather than clasp the stems. Microscopically *F. flaccida* differs from *M. deppei* in having non-decurrent leaves with sharply toothed margins, serially papillose leaf cells, and more weakly developed alar cells.

Hampe (1862a) published a preliminary paper on mosses collected by A. Lindig in Colombia between 1859 and 1861. In that paper he proposed several new species, many of which he described fully in a later paper (Hampe 1862b). All the new names proposed in the earlier paper are invalid since they lack descriptions. *Pilotrichella fusco-viridis* was proposed by Hampe (1862a), but in the later paper this same taxon was described as *Neckera fusco-viridis.* Hampe based these two names on different specimens, even though he had in mind only one taxon, which can be seen by his citation of both collections in a later publication (Hampe 1865).

2. *Meteorium laevifolium* Mitt., J. Linn. Soc., Bot. 12: 441. 1869. *Papillaria laevifolia* (Mitt.) Broth. *ex* Paris, Coll. Nom. Broth. 23. 1909. Protologue. Ins. Jamaica ? ex *Herb. Brown.* Venezuela, ex *Herb. Dozy.* Andes Quitenses, in monte Tunguragua ad pagum Baños (6000 ped.), *Spruce, n. 1255, 1256.*

Papillaria squamatula Müll. Hal. *ex* Ångstr., Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 33(4): 34. 1876. Protologue. [Caldas, Brasiliae] *Henschen* collegit.

Plants slender, in light green, yellow green, or golden red, stiff, pendent masses. Stems pendent, irregularly but densely branched, branch tips at times attenuate, not stipitate, to 10 cm long; stems in cross section with sclerodermis of 3–5 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, firm-walled, central strand weakly developed; paraphyllia absent; pseudoparaphyllia foliose; rhizoids sporadically developed, in dense groups, dark brown to blackish, smooth, not branched, from clusters of initials abaxial to the leaf insertions. Stem leaves ovate-triangular, strongly auriculate, 1.2–2.0 mm long; branch leaves ovate to ovate-triangular, moderately auriculate, 0.8–1.2 mm long, plane, clasping at base, erect to imbricate with spreading apices when dry, erect-spreading when wet, acuminate, at times ending in a short, hyaline hair-point, yellow at base, shortly decurrent; margins plane, bordered by long, narrow, smooth cells at base, sharply serrate below, papillose-crenulate above; costae single, ending above midleaf, in cross section cells homogeneous, thick-walled; upper and median cells densely seriate pluripapillose over the cell lumina, oval to elongate, thick-walled, somewhat porose, 12–24 × 4–5 µm, cells near the costa longer; extreme basal cells elongate, usually porose, smooth; alar cells quadrate to rectangular, thick-walled, porose, restricted to a few cells at the basal angles. Asexual reproduction by deciduous flagelliform branches. Dioicous. Sporophytes unknown from Central America, description from Venezuela (*Steyermark & Liesner 118362B*, MO). Perigonia gemmate, lateral on stems and branches. Vaginulae densely hairy. Setae flexuose, yellowish red, lightly roughened above, 3–5 mm long. Capsules erect, oblong to short-cylindric, 1.5–2.0 mm long; exothecial cells short-rectangular, firm-walled, not collenchymatous; stomata on neck; opercula conic-rostrate, 1.0 mm long; annuli rudimentary; peristome diplolepideous, reddish yellow; exostome teeth narrowly triangular, papillose throughout; endostome

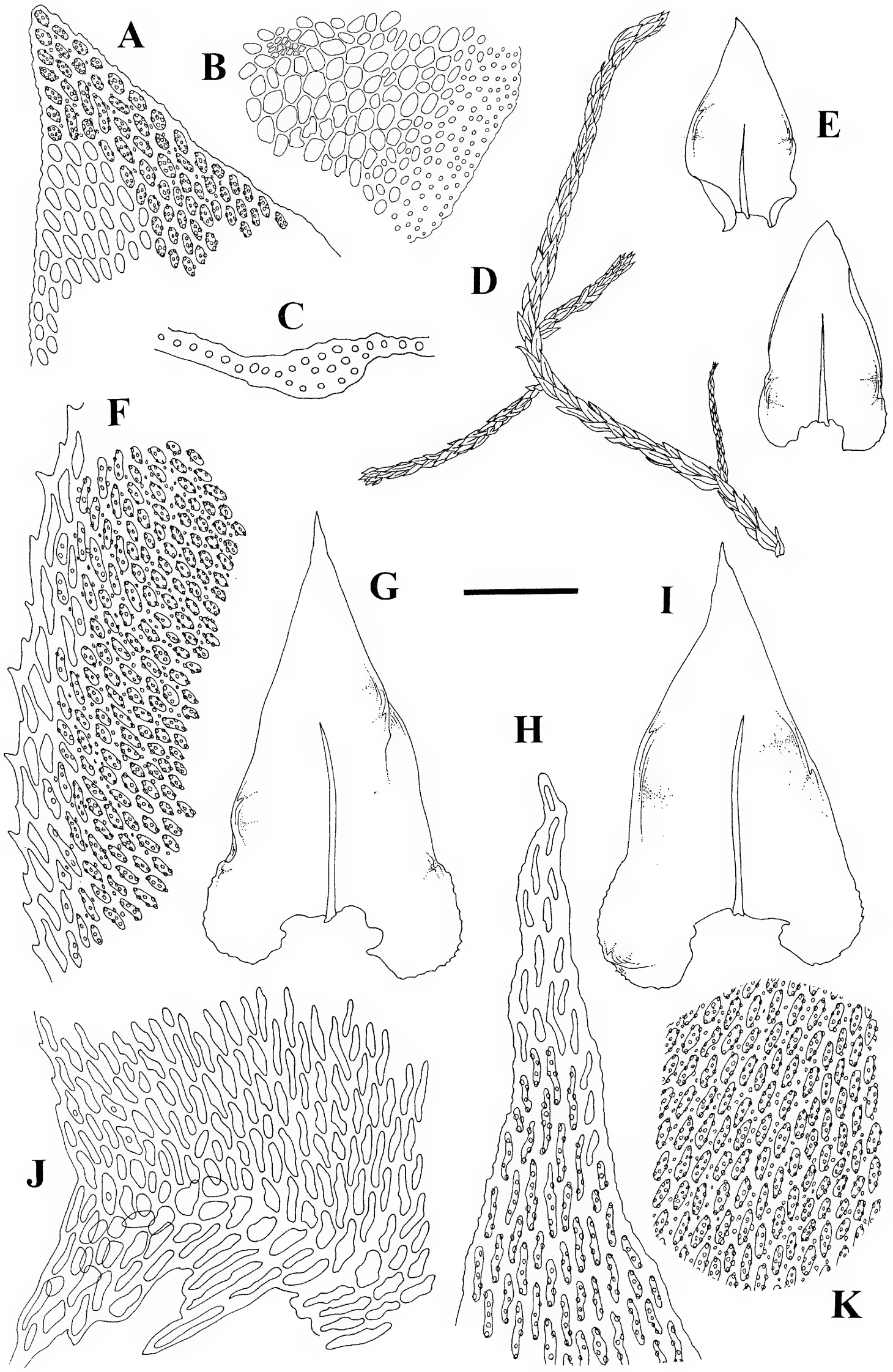


Figure 40. *Meteorium laevifolium*. A. Branch leaf apex. B. Stem in cross section. C. Costa in cross section. D. Habit. E. Branch leaves. F. Median leaf cells and margin. G & I. Stem leaves. H. Stem leaf apex. J. Leaf alar region. K. Median leaf cells. Scale in mm: bar = 0.05 (A, C, F, H, J, K); bar = 0.08 (B); bar = 0.5 (E, G, I); bar = 2.6 (D). B, C from *Stevens 18250*; F, H, J, K from *Croat 26639*; all other figure parts from *Allen 12424*.

papillose, basal membranes short, segments linear, perforate, cilia absent. Spores round, lightly papillose, 12–20 µm. Calyptrae cucullate, densely hairy, 2 mm long.

Illustrations. Buck (1998, Pl. 105, as *Cryptopapillaria penicillata*). Figure 40.

Habitat. Epiphyte on tree trunks and vines; 1000–2250 m.

Distribution in Central America. HONDURAS. Olancho: *Allen 12424* (MO). COSTA RICA. Puntarenas: *Croat 26639* (MO). PANAMA. Chiriquí: *Stevens 18250* (MO, NY).

World range: Central America; Caribbean; Western and Northern South America, Brazil.

Dry plants of *M. laevifolium* have smooth, imbricate leaves that give the species an appearance usually associated with species of *Braunia* or *Cryphaea*. The densely pluripapillose leaf cells of *M. laevifolium* quickly separate it from those genera. Within *Meteorium* this species is distinguished by a combination of its small size and smoothly imbricate leaves that are strongly auriculate and have densely verruculose-papillose leaf cells. *Meteorium laevifolium* has been widely confused with *Cryptopapillaria penicillata* (Dozy & Molk.) M. Menzel, *e.g.*, all Neotropical material at MO named *Cryptopapillaria penicillata* is actually *Meteorium laevifolium.* Buck (1998) tentatively synonymized them, but the two species are not very similar. In *C. penicillata* the leaves are loosely erect rather than imbricate when dry and the leaf apices are twisted in a distinctive way, similar to the apices of *Toloxis imponderosa.* Most importantly, the leaf cells in *C. penicillata* are pluripapillose with the papillae arranged over the cell walls rather than the cell lumina. The sporophytes of *C. penicillata* differ from those of *M. laevifolium* in having immersed capsules with very long, linear-lanceolate perichaetial leaves. In addition, *C. penicillata* has mitrate calyptrae.

3. *Meteorium nigrescens* (Hedw.) Dozy & Molk., Musci Frond. Ined. Archip. Ind. 160. 1848. *Hypnum nigrescens* Sw. *ex* Hedw., Sp. Musc. Frond. 250. 1801. *Pterogonium nigrescens* (Hedw.) Sw., Fl. Ind. Occid. 3: 1778. 1806. *Pterigynandrum nigrescens* (Hedw.) Brid., Muscol. Recent. Suppl. 4: 130. 1819 [1818]. *Neckera nigrescens* (Hedw.) Schwägr., Sp. Musc. Frond. Suppl. 3(1)2: 244. 1828. *Papillaria nigrescens* (Hedw.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 265. 1877. *Tricholepis nigrescens* (Hedw.) Grout, Moss Fl. N. Amer. 3(4): 214. 1934. Protologue. In insulis Jamaicae legit *D. O. Swartz.*

Neckera appressa Müll. Hal., Syn. Musc. Frond. 2: 136. 1850, new name for *Hypnum appressum* Hornsch., Fl. Bras. 1(2): 90. 1840, illegitimate homonym, not *Hypnum appressum* Brid., 1812. *Meteorium appressum* (Müll. Hal.) Mitt., J. Linn. Soc., Bot. 12: 443. 1869. *Papillaria appressa* (Müll. Hal.) Ångstr., Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 33(4): 34. 1876. Protologue. [Brazil] In prov. Minarum [Minas Gerais] ad terram: M[artius].

Papillaria nigrescens var. *donnellii* Austin, Musci Appalach., Suppl. 1: 533. 1878. *Papillaria nigrescens* subsp. *donnellii* (Austin) Kindb., Canad. Rec. Sci. 6: 19. 1894. *Tricholepis nigrescens* var. *donnellii* (Austin) Grout, Moss Fl. N. Amer. 3: 214. 1934. Protologue. [United States] Trunks of trees, West Florida, *J. Donnell Smith.* Type. Trunks of trees, West Florida, *J. Donnell Smith* (MO, isotype).

Plants slender to medium-sized, green or yellow green, often jet black tinged, in stiff or soft tufts, mats, or pendent masses. Stems erect, horizontal or pendent, irregularly to pinnately branched, stem and branch tips at times attenuate, not stipitate, to 10 cm long; stems in cross section with scleroderm of 2–5 rows of small, yellow or red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, firm-walled, central strand weakly developed; paraphyllia absent; pseudoparaphyllia foliose, cells papillose; rhizoids in dense groups, reddish brown, smooth, not branched, from circular clusters of initials abaxial to the leaf insertions; axillary hairs 4–6 cells long, 1–2 short, brown, basal cells and 3–4 short, rounded, hyaline, upper cells. Stem leaves somewhat larger and broader than branch leaves with more strongly cordate bases; branch leaves typically erect-appressed when dry, but occasionally leaves loosely spreading, to wide-spreading when wet, typically ovate-triangular, at times lanceolate, 1.1–1.7 mm long, gradually short- to long-acuminate, at times with long, hyaline hair-points, concave, shallowly plicate, cordate at base, decurrent; margins plane or with erect to narrowly recurved upper margins, entire throughout or with projecting papillae above, crenulate at base; costae single, ending at midleaf, in cross section cells with superficial guide cells somewhat enlarged, other cells homogeneous and thick-walled; cells densely pluripapillose with 3–7 papillae scattered over the cell

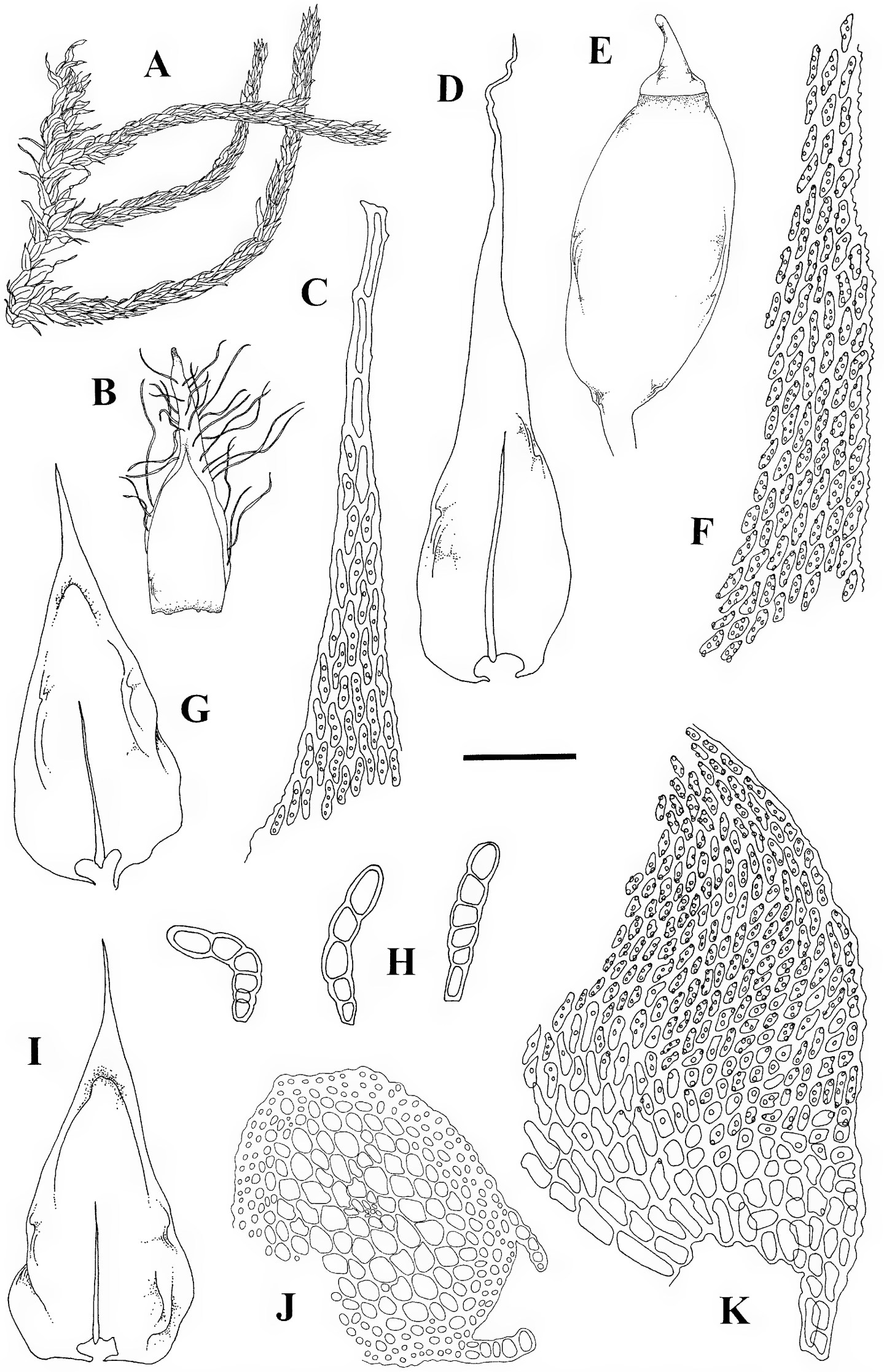
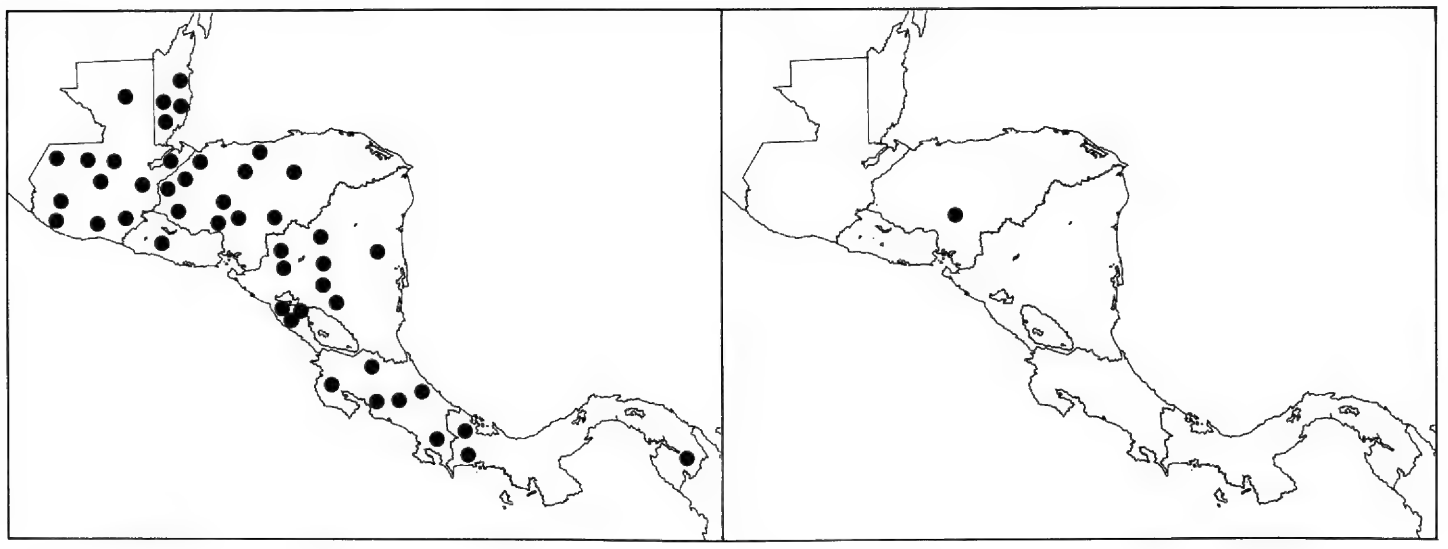


Figure 41. *Meteorium nigrescens*. A. Habit. B. Calyptra. C. Stem leaf apex. D. Stem leaf. E. Seta, capsule, and operculum. F. Median leaf cells and margin. G & I. Branch leaves. H. Axillary hairs. J. Stem in cross section. K. Basal leaf cells. Scale in mm: bar = 0.04 (H); bar = 0.05 (C, F, K); bar = 0.08 (J); bar = 0.41 (D, G, I); bar = 0.9 (B, E); bar = 3.2 (A). A from *Allen 13736*; all other figure parts from *King C-74-024*.



Meteorium nigrescens *Meteorium teres*

lumina, upper cells rhombic to linear, firm-walled, 8–26 × 3–5 µm, median cells fusiform to linear; basal cells near costa linear, more or less smooth; cells in cordate base rhombic to fusiform, median cells at insertion short-rectangular, smooth; alar cells quadrate to subquadrate, smooth, thick-walled. Asexual reproduction by deciduous flagelliform branches or caducous leaves. Dioicous. Perigonia lateral, gemmate, to 1 mm long. Perichaetia lateral, 1–1.5 mm long; paraphyses numerous, becoming thick-walled and bi- to multiseriate. Vaginulae densely hairy. Setae long, flexuose, yellowish red, slightly roughened, 5–8 mm long. Capsules erect, elliptic to short-cylindric, 2.0–2.5 mm long; exothecial cells oblate in 3–5 rows at mouth, lower cells short-rectangular to subquadrate, firm-walled, not collenchymatous; stomata superficial on neck; opercula obliquely long-rostrate, 0.7–1.3 mm long; annuli rudimentary, of quadrate, thick-walled cells; peristome diplolepideous, yellowish white; exostome teeth narrowly triangular, papillose throughout, median line thickened; endostome papillose, basal membranes low, segments linear, not perforate, cilia absent or rudimentary. Spores irregularly rounded, lightly papillose, 14–30 µm. Calyptrae cucullate, densely hairy, 2.0–2.5 mm long.

Illustrations. Hedwig (1801, Pl. 65); Schwägrichen (1828, Pl. 244b); Grout (1934, Pl. 63 A–B); Breen (1963, Pl. 106); Florschütz (1964, Fig. 101); Bartram (1949, Fig. 119 C–E); Spessard (1980, Fig. 12); Crum and Anderson (1981, Fig. 383 F–I); Reese (1984, Fig. 44 A–B); Sharp *et al.* (1994, Fig. 546); Churchill and Linares (1995, Fig. 125 a–g); Duarte Bello (1997, Pl. 200); Buck (1998, Pl. 104); Buck (2003, Fig. 124). Figure 41.

Habitat. On tree roots, trunks, branches, twigs, vines, fallen branches, logs, roof thatch, soil banks, rocks, boulders, and cement culvers, sea level to 1800 m.

Distribution in Central America. BELIZE. Belize: *Lundell 1980* (FH); Cayo: *Allen 18011* (BRH, MO); Stann Creek: *Gentle 2140* (FH); Toledo: *Allen 18754* (MO). GUATEMALA. Alta Verapaz: *Croat 41505* (GUAT, MO, NY); Baja Verapaz: *Sharp 2895* (FH, MO); Huehuetenango: *Steyermark 49654* (F, FH); Izabal: *Jones & Facey 3348* (FH, MO, NY); Jutiapa: *Standley 75553* (F, FH); Petén: *Lundell 2123* (FH, MO, US); Quetzaltenango: *Spellman et al. B111c* (MO); Quiché: *Sharp 2549* (FH); Retalhuleu: *Standley 87886* (F, FH); Santa Rosa: *Standley 78188* (F, FH); Zacapa: *Croat 41872* (GUAT, NY, MO). EL SALVADOR. San Salvador: *Standley 22456a* (US). HONDURAS. Atlántida: *Allen 17286* (MO, TEFH); Comayagua: *Allen 13736* (MO, TEFH); Copán: *Allen 17703* (MO, TEFH); Cortés: *Croat 42763* (MO, NY, TEFH, US); El Paraíso: *Molina & Molina 27895B* (F, MO); Francisco Morazán: *Standley 15037* (F); La Paz: *Allen 14551* (FH, MO, TEFH); Lempira: *Allen 11165* (MO, TEFH); Olancho: *Allen 12432* (MO, TEFH); Santa Bárbara: *Allen 11809* (FH, MO, TEFH); Yoro: *Allen 13574* (MO, TEFH). NICARAGUA. Boaco: *Stevens 5912* (HNMN, MO, NY); Chontales: *Stevens 2860B* (MO); Estelí: *Stevens 16292* (MO, HNMN); Granada: *Cerda & Moreno GC-1519* (DUKE, MO); Jinotega: *Stevens 16451* (MO); Madriz: *Moreno 2841* (MO); Managua: *Standley 8149* (F); Masaya: *Standley & Garnier 8118* (F); Matagalpa: *Guzmán & Castro 1410* (F, HNMN, MO, NY, US); Zelaya: *Pipoly 4570* (MO, HNMN). COSTA RICA. Alajuela: *Liesner 4740b* (MO); Cartago: *Dodge 3947* (F, FH, MO, US); Guanacaste: *Standley & Valerio 45944* (FH, US);

Limón: *Croat 43161* (CR, MO); Puntarenas: *Crosby 2703* (MO); San José: *King C-74-024* (CR, MO, NY). PANAMA. Bocas del Toro: *Crosby 4086* (MO); Chiriquí: *Croat 26771* (MO, PMA, NY, US); Darién: *Allen 8823* (MO).

World range: Southeastern U.S.A.; Mexico; Central America; Caribbean; Western, Northern, and Southern South America, Brazil.

Meteorium nigrescens is a common moss in Central America, where it grows on a wide variety of habitats. The species is exceedingly variable and its extreme expressions appear to be distinct. There are, however, numerous intermediate forms and, as noted by Bartram (1949), "The variations of this plastic species are legion and I doubt if any practical purpose would be served in trying to segregate them here." When growing on the ground, rocks, or tree trunks the species usually has stiffly erect, plicate leaves and numerous closely spaced branches. This form of the species has ovate-triangular, narrowly acuminate leaves that only rarely end in hyaline hair-points. In epiphytic habitats, especially when the plants grow pendent, they are more lax in aspect and have narrowly ovate-lanceolate leaves that often have hyaline hair-points. In some collections the leaves end in long, hyaline capillary hair-points. The stiffly erect form of the species at times has microphyllous flagellate branches that arise in the leaf axils. These flagellate branches can be copiously present. The lax, long hair-pointed form of the species often has strongly caducous leaves resulting in branches and stems that are nearly naked, except for small clusters of leaves at the tips.

Meteorium deppei is usually a larger plant than *M. nigrescens*, but the two species have similar pendent forms with a lax aspect and leaves that consistently have very long, capillary hair-points. *Meteorium deppei* differs consistently from all forms of *M. nigrescens* in having elongate to linear cells filling its cordate leaf bases. In *M. nigrescens* the cells in the cordate leaf bases are subrectangular to rhombic. *Meteorium nigrescens*, *M. laevifolium*, and *Toloxis imponderosa* are all similar in size. These last two species differ from *M. nigrescens* in having strongly auriculate leaves. In addition, *Meteorium laevifolium* has smoothly terete leaves with verruculose-papillose leaf cells. *Toloxis imponderosa* further differs from *M. nigrescens* in having strongly and consistently twisted leaf apices.

Meteorium nigrescens is presently known only from the Western Hemisphere. The species was reported from Java by Dozy and Molkenboer (1848), but Fleischer (1908) considered the collections on which the records are based to be *Papillaria leuconeura* (Müll. Hal.) A. Jaeger (≡ *Meteorium leuconeurum*). Brotherus (1929) recorded *P. nigrescens* and *P. appressa* from China, but Noguchi (1971) considered these collections to be *Meteorium papillarioides* Nog.

4. *Meteorium teres* Mitt., J. Linn. Soc., Bot. 12: 438. 1869. *Pilotrichella teres* (Mitt.) Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 225. 1872. *Papillaria teres* (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 269. 1877. Protologue. Mexico, Xalapa, *Harris, Deppe et Schiede, m. 1093*; Oaxaca, *Galeotti, n. 6887*. Type (see Spessard 1980). Mexico, *Harris* (NY, lectotype).

Plants medium-sized to robust, in dull green or yellow green, at times jet black tinged, mats. Stems creeping or horizontal, irregularly branched, not stipitate, to 10 cm long; stems in cross section with sclerodermis of 2–5 rows of small, yellow or red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, firm-walled, central strand weakly developed; paraphyllia absent; pseudoparaphyllia foliose, cells smooth; rhizoids sparsely developed, reddish brown, smooth, not branched, from dense circular clusters of initials abaxial to the leaf insertions; axillary hairs 4–6 cells long, 2 short, red brown, basal cells, 2–4 short, rounded, hyaline upper cells. Stem leaves erect when dry, erect-turgid when wet, 2–3 mm long, oblong-obovate, strongly concave to cucullate, short- to long-acuminate, at times ending in hyaline hair-points, clasping and cordate to auriculate at base, decurrent; margins plane or incurved, often wavy, upper margins crenulate by projecting papillae, basal margins crenulate to serrulate by projecting cell end walls and projecting papillae; costae single, ending above midleaf; upper leaf cells fusiform to linear, with 1–3 papillae, 15–40 × 3–5 mm; median cells linear, with 1–2 papillae, 25–70 × 3–5 mm; basal leaf cells oblong to rectangular, often smooth and porose, cells in the auriculate base linear; alar cells weakly developed, subquadrate, smooth, firm-walled, often porose. Branch leaves oblong-ovate, erect-appressed when dry, erect and turgid when

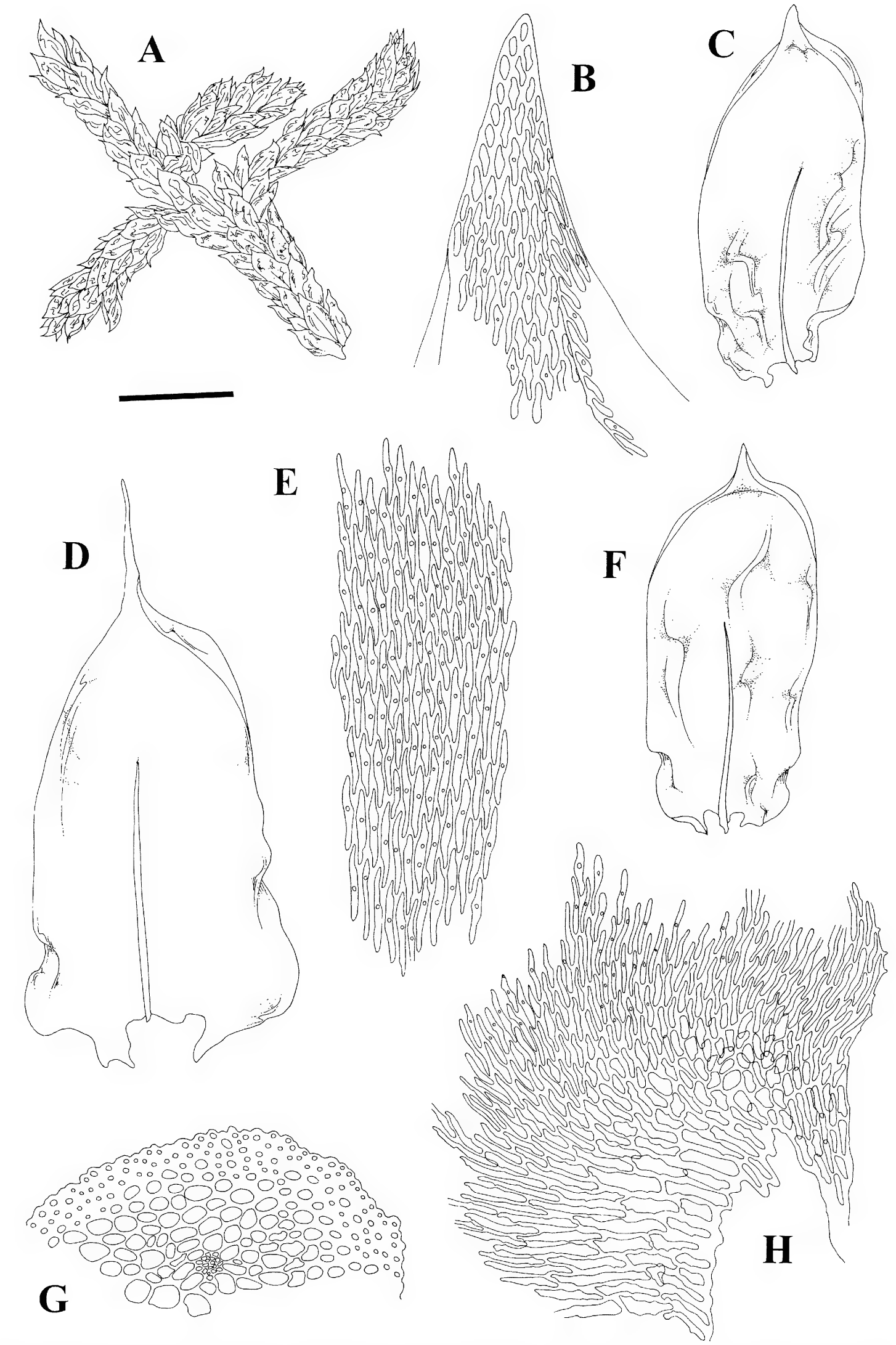


Figure 42. *Meteorium teres*. A. Habit. B. Branch leaf apex. C & F. Branch leaves. D. Stem leaf. E. Median leaf cells. G. Stem in cross section. H. Basal leaf cells and alar region. Scale in mm: bar = 0.06 (B, E, G, H); bar = 0.9 (C, D, F); bar = 4 (A). All figure parts from *Pilz & Pilz 1413*.

wet, 1.5–3.0 mm long, short-acuminate to apiculate, strongly concave, cucullate above, smooth, cordate at base, decurrent; margins erect or incurved, crenulate by projecting papillae; costae single, ending at or a little above midleaf, in cross section cells with superficial guide cells somewhat to not enlarged, other cells homogeneous and thick-walled; upper leaf cells fusiform to linear, with 1–2 papillae, 10–40 × 3–5 μm; median cells linear, 30–60 × 3–5 μm, with 1–2 papillae; basal cells oblong to rectangular, 17–40 × 5–10 μm, often smooth and porose, cells in cordate base elongate to linear; alar cells weakly developed, subquadrate, smooth, firm-walled, often porose. Dioicous. Sporophytes not seen, description from Spessard (1980). Setae scabrous, 5.0–8.0 mm long. Capsules ovoid to oblong-ovoid, 1.5–2.5 mm long; opercula obliquely rostrate; annuli small or lacking; peristome diplolepideous, pale; exostome teeth narrowly triangular, papillose; endostome papillose, basal membranes low, segments linear, cilia rudimentary. Spores slightly ovoid, roughened, 13–26 μm. Calyptrae cucullate, densely hairy.

Illustrations. Spessard (1980, Fig. 10); Sharp *et al.* (1994, Fig. 543). Figure 42.
Habitat. Terrestrial, growing on litter; 1800 m.
Distribution in Central America. HONDURAS. Francisco Morazán: *Pilz & Pilz 1413* (MO).
World range: Mexico; Central America; Western South America.

Meteorium teres is a large-sized species with turgid stems and branches. When wet its leaves are smoothly turgid, but because they are so deeply concave the dry leaves have a wrinkled appearance. Most collections of *M. deppei* can be distinguished from *M. teres* by their plicate, long hair-pointed leaves. There are, however, forms of *M. deppei* with smooth leaves, and the stem leaves of *M. teres* are sometimes very long-acuminate or even hair-pointed. *Meteorium teres* and *M. deppei* are best distinguished by branch leaf differences. In *M. teres* the branch leaves, especially those in the apical buds, are consistently apiculate to short-acuminate, while those of *M. deppei* are long-acuminate to hair-pointed. *Meteorium laevigata* is similar to *M. teres* in having imbricate leaves, but it is smaller in size, with smoothly imbricate leaves and densely verruculose-papillose leaf cells. *Meteorium nigrescens* is also a smaller plant than *M. teres*, and it has stiffly erect-imbricate leaves with short cells in the cordate leaf bases.

Meteorium teres is present throughout eastern Mexico, but it is known in Central America from a single Honduran collection. The species is also known from two Ecuadorian localities: An Bäumen in feuchten Waldgebieten, am Vulkan Tunguragua, 1800–2800 m, 15 Dezember. 1880, [*F. Lehmann*] *N⁰ 697* (Bescherelle 1894), and Andes de Quito, *Jameson* 1851 (MO). In view of its large size and distinctive aspect, it is difficult to explain the oddly dissected range of *M. teres* as an artifact of undercollecting.

7. *Squamidium* (Müll. Hal.) Broth., Nat. Pflanzenfam. I(3): 807. 1906.

Meteorium sect. *Squamidium* Müll. Hal., Linnaea 42: 420. 1879.

Plants predominantly creeping or pendent, shiny green to yellow green, more or less tinged brown or black when old. Primary stems adnate to the substrate; stems in cross section with several rows of small, thick-walled epidermal cells, cortical cells enlarged, thin-walled, central strand weakly developed; rhizoids yellow to red brown, smooth, not branched, from circular clusters of initials abaxial to the leaf insertions; paraphyllia absent; pseudoparaphyllia absent; scale leaves present. Secondary stems horizontal to erect, irregularly or pinnately branched, at times elongating into filiferous branches. Leaves dimorphic or trimorphic, more or less clasping the stems, strongly decurrent; costae single and weak (at times some leaves with double costae or ecostate), 1/2–3/4 the leaf length, in cross section cells homogeneous, usually consisting of two cell layers; cells smooth, firm-walled, elongate throughout except in the alar regions; alar cells strongly differentiated, quadrate to rectangular, thin- to thick-walled. Dioicous. Perigonia and perichaetia lateral on branches. Capsules immersed or exserted, ellipsoid; exothecial cells irregularly rectangular, firm-walled, those near the mouth quadrate to oblate; stomata superficial on neck; opercula short-rostrate; annuli rudimentary; peristome diplolepideous; exostome teeth linear, papillose throughout or smooth; endostome with high basal membranes, linear segments, cilia rudimentary or absent. Calyptrae mitrate, hairy.

Squamidium is a genus of predominantly epiphytic, frequently pendulous mosses of tropical and subtropical American-African distribution. There are seven species of *Squamidium* distributed in two sections: sect. *Squamidium*, with immersed capsules and entire to weakly serrate stolon leaf margins; sect. *Macrosquamidium* Broth., with exserted capsules and stolon leaf margins strongly serrate by recurved teeth. All seven are found in the Neotropics, and one of those (*S. brasiliense*) occurs disjunctly in Africa. There are six species of *Squamidium* in Central America: (sect. *Squamidium*) *S. isocladum*, *S. leucotrichum*, *S. livens*, and *S. nigricans*; (sect. *Macrosquamidium*) *S. diversicoma* and *S. macrocarpum*. Characters that are important at the generic level in *Squamidium* include its linear, papillose exostome teeth; mitrate calyptrae; densely foliate and strongly decurrent leaves; single costae that usually have only two cell layers; linear-flexuose, smooth leaf cells; strongly differentiated alar cells; and the tendency for the leaves and stems to become blackened with age. Within the Meteoriaceae *Squamidium* appears closely related to *Zelometeorium*, *Meteoridium*, and *Meteorium*. All three genera differ from *Squamidium* in having weakly developed alar cells. In addition, *Zelometeorium* has squarrose to squarrose-recurved leaves, *Meteoridium* has cross-striate exostome teeth, and *Meteorium* has papillose leaf cells.

Buck (1994a, 1998) placed *Squamidium* in the Lembophyllaceae on the basis of its smooth leaf cells and well-differentiated alar cells. *Squamidium* and other Meteoriaceae genera with smooth leaf cells have also been placed in the Brachytheciaceae (Buck & Goffinet 2000). Allen and Magill (2003) returned *Squamidium* to the Meteoriaceae on the basis of its weak, single costae; the ability of the plants to produce an intense black coloration; stoloniferous growth form; mitrate calyptrae; and reduced peristome with linear, papillose exostome teeth. *Squamidium* was revised by Allen and Crosby (1986b).

The name *Squamidium* combines the Latin *squama* (scale) with the Greek diminutive suffix *-idium*, and may refer to its imbricate, scale-like stem leaves.

1. Leaves hair-pointed . . . . . 3. *S. leucotrichum*
1. Leaves acute or acuminate 2

2. Leaves cordate at base; alar cells thin-walled, excavate, confined to area at leaf insertions; plants often with filiform branches . . . . . 4. *S. livens*
2. Leaves not cordate at base; alar cells thin- or firm-walled, reaching or extending up the margins; filiform branches infrequent 3

3. Branch leaves imbricate; alar cells quadrate to oblate, firm-walled . . . . . 1. *S. diversicoma*
3. Branch leaves loosely erect; alar cells shortly rectangular to square, usually lax, at times more or less firm-walled 4

4. Stem leaves short-acuminate; branch leaves serrulate above; margins broadly incurved above and usually meeting below an apiculate to shortly acuminate, recurved apex; apex not galeate . . . . . 6. *S. nigricans*
4. Stem leaves hair-pointed; branch leaves entire or weakly serrulate above; margins erect, slightly recurved; apex broadly acute to short-acuminate, frequently galeate 5

5. Stolon leaves with strongly recurved marginal teeth extending from the leaf apex to the shoulders . . . . . 5. *S. macrocarpum*
5. Stolon leaves entire or with a few short marginal teeth on the leaf apex, if present the teeth neither recurved nor extending onto the leaf shoulders . . . . . 2. *S. isocladum*

1. *Squamidium diversicoma* (Hampe) Broth., Nat. Pflanzenfam. I(3): 809. 1906. *Neckera diversicoma* Hampe, Vidensk. Meddel Dansk. Naturhist. Foren Kjøbenhaven ser. 4, 1: 114. 1879. *Papillaria diversicoma* (Hampe) Kindb., Enum. Bryin. Exot. 102. 1891. Protologue. [Brazil] In vicinia Rio de Janeiro parce legit *Glaziou 9281*. Types (see Allen & Crosby 1986b). BM, lectotype; G, H, PC, isolectotypes.

Squamidium diversifolium R. S. Williams, Bull. New York Bot. Gard. 6(21): 239. 1909. Protologue. [Bolivia] On Pelichuco River below Pelichuco, 2600 meters elevation, April 30, 1902 ([*Williams*] *2856*). Tigrepata, 1500 meters, Feb. 12, 1902 ([*Williams*] *2137*). Types (see Allen & Crosby 1986b). *Williams 2856* (NY, lectotype; BM, FH, H, isolectotypes); *Williams 2137* (BM, H, NY, syntypes).

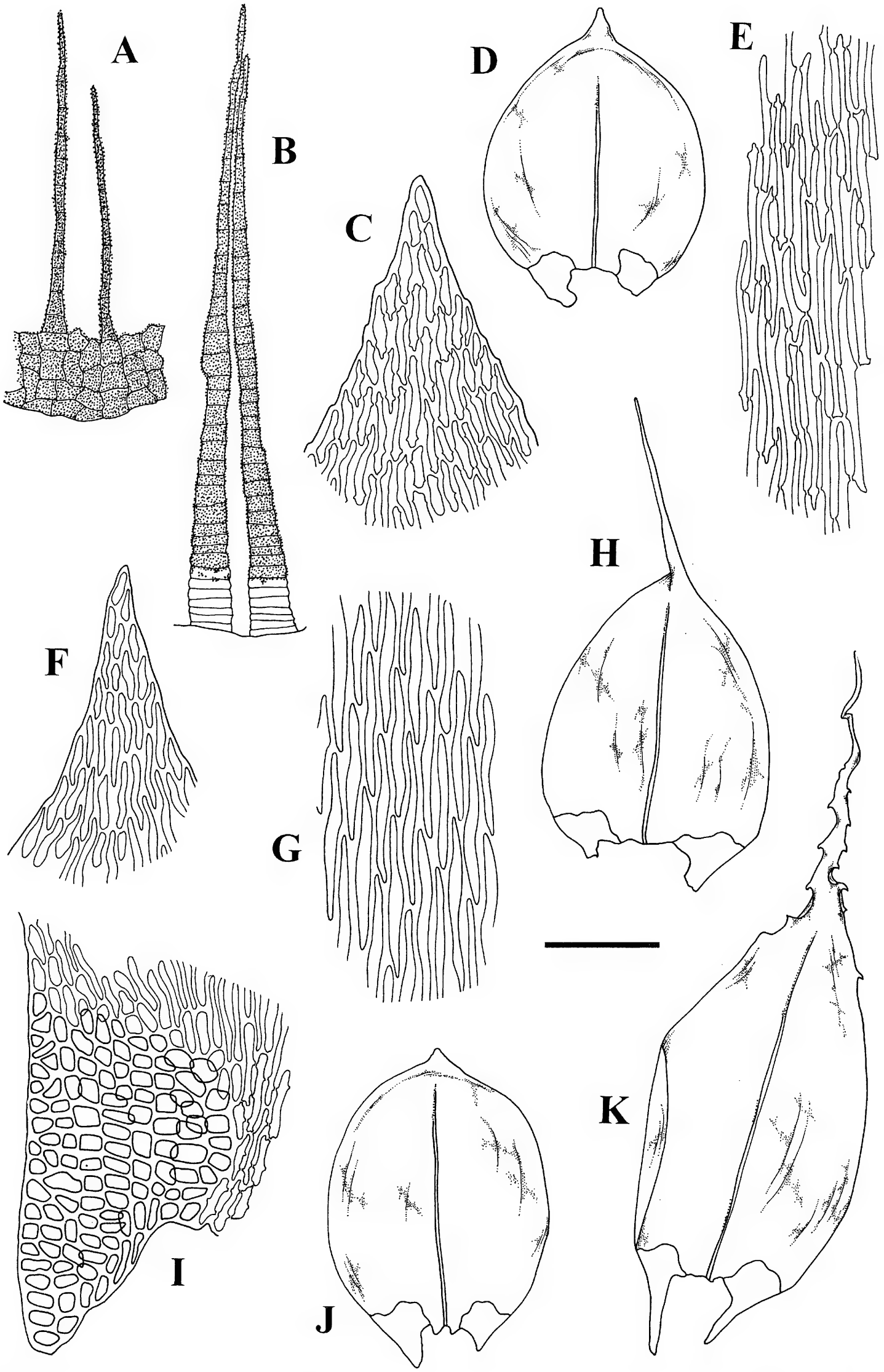
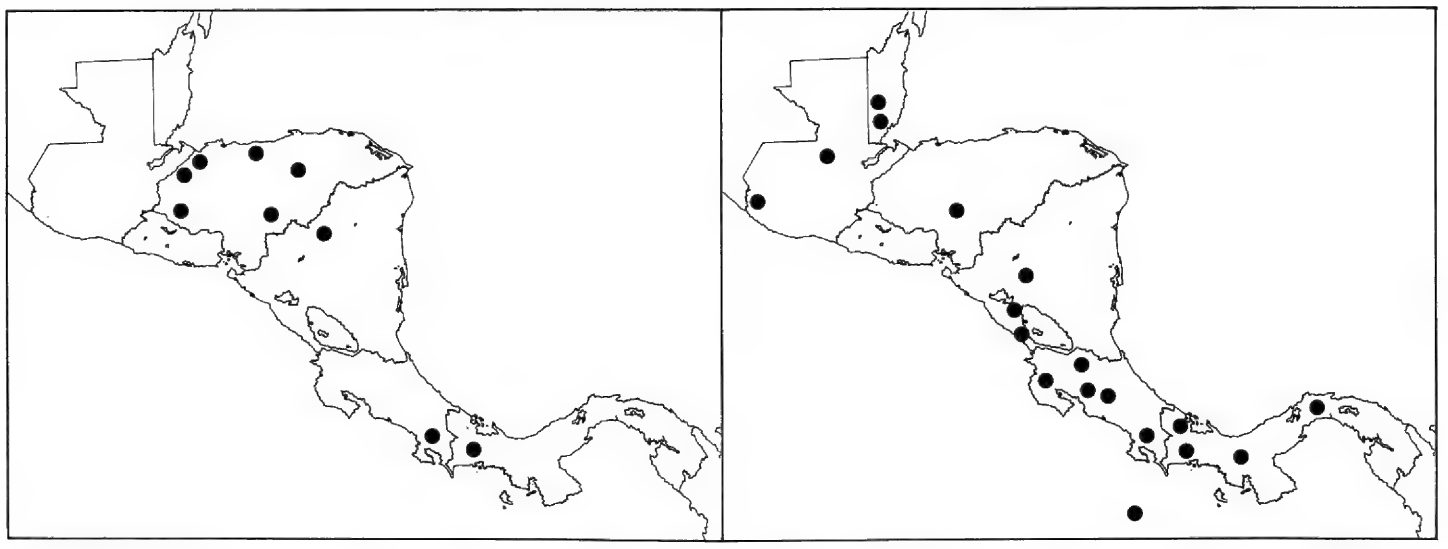


Figure 43. *Squamidium diversicoma*. A. Endostome, ventral (inner) surface. B. Exostome, ventral (inner) surface. C & F. Leaf apices. D & J. Branch leaves. E & G. Median leaf cells. H. Stem leaf. I. Alar cells. K. Stolon leaf. Scale in mm: bar = 0.05 (A, B); bar = 0.06 (C, E, F, G, I); bar = 0.6 (D, H, J, K). All figure parts from *Crosby 3975*.



Squamidium diversicoma *Squamidium isocladum*

Squamidium chiriquense Crosby, Ann. Missouri Bot. Gard. 58: 89. 1971. Protologue. Panama. Chiriquí: About 2 miles S of Boquete. *Crosby 3975*. Types. Panama. Chiriquí: About 2 miles S of Boquete. *Crosby 3975* (MO, holotype; DUKE, U, isotypes).

Plants slender to medium-sized, creeping or pendent, epiphytic. Primary stems to 15 cm long; stems in cross section with 1–3 rows of small, thick-walled, yellow to red epidermal cells, cortical cells enlarged, thin-walled, hyaline, central strand small. Secondary stems pendent, erect or becoming adnate to the substrate, identical to primary stems, irregularly or weakly pinnately branched, branches to 1.5 cm long, at times elongating into filiferous branches to 4 cm long. Leaves trimorphic: stolon leaves, primary stem leaves, and branch leaves. Stolon leaves 1.7–3.0 × 0.3–1.0 mm, ovate-lanceolate; upper margins dentate or with recurved teeth. Primary stem leaves erect-appressed, 1.5–3.0 × 1.0–1.2 mm, orbicular to broadly ovate below, abruptly acuminate above, strongly decurrent; margins entire or weakly serrulate above; costae single, weak; median cells linear-flexuose, 90–130 × 4–5 µm, firm-walled, not porose; alar cells strongly differentiated, short-rectangular, quadrate or oblate, thick-walled. Branch leaves imbricate to julaceous, 0.6–2.0 × 0.4–1.0 mm, broadly ovate to elliptic-ovate, shortly acute to cuspidate, usually galeate; margins plane below, erect to incurved above, serrulate above or entire throughout. Dioicous. Setae yellow red to dark red, 1.5–2.0 mm long, smooth. Capsules exserted, erect, ellipsoid, 2.5–3.0 mm long; exothecial cells quadrate to oblate at the mouth, irregularly rectangular below, firm-walled; stomata on neck; opercula 1.0–1.5 mm long, shortly rostrate; annuli rudimentary, deciduous, of several rows of thick-walled cells; exostome teeth linear, papillose; endostome lightly papillose, basal membranes 0.08–0.09 mm high, segments linear, not perforate, cilia rudimentary or absent. Spores round, 16–32 µm, lightly papillose. Calyptrae mitrate, 3 mm long, densely hairy.

Illustrations. Crosby (1971, Figs. 1–3); Allen and Crosby (1986b, Figs. 73–89, 91); Sharp *et al.* (1994, Fig. 539 e–g). Figure 43.

Habitat. Epiphytic, on trunks, branches, and twigs of trees and shrubs; 500–1800 m.

Distribution in Central America. HONDURAS. Atlántida: *Allen 17598* (MO, TEFH); Cortés: *Morton 7638a* (US); El Paraíso: *Molina & Molina 27895c* (MO); Lempira: *Allen 11131* (MO); Olancho: *Allen 12441* (MO); Santa Bárbara: *Crosby 2788* (DUKE, MO). NICARAGUA. Jinotega: *Standley 10204* (F, FH, G). COSTA RICA. Puntarenas: *Crosby 3596* (MO). PANAMA. Chiriquí: *Allen 7986* (MO).

World range: Mexico; Central America; Western and Northern South America, Brazil.

Squamidium diversicoma and *S. macrocarpum* (the only species in sect. *Macrosquamidium*) differ from all other Central American species of *Squamidium* in having exserted capsules and stolon leaf margins with recurved teeth. Plants of *S. macrocarpum* are much larger than those of *S. diversicoma*, and they further differ in having loosely erect branch leaves with shortly rectangular, bulging, laxly thin-walled alar cells. *Squamidium diversicoma* also differs from the other Central American

species of *Squamidium* in having imbricate branch leaves with incrassate, quadrate to oblate, alar cells. *Squamidium leucotrichum* further differs from *S. diversicoma* in having long, hair-pointed leaves, while *S. nigricans* differs in having branch leaves with consistently serrulate upper margins that are broadly incurved above.

Collections of *Squamidium diversicoma* often have long, attenuate branches with leaves that are identical to the stolon leaves: ovate-lanceolate, tortuose above, and with recurved teeth extending onto the shoulders. The attenuate branches are on the pendent parts of the plants and are similar in form to the stoloniferous shoots of *Barbellopsis trichophora*.

2. *Squamidium isocladum* (Renauld & Cardot) Broth., Nat. Pflanzenfam. I(3): 809. 1906. *Pilotrichella isoclada* Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32(1): 180. 1894. Protologue. [Costa Rica] Sur les branches d'un arbrisseau à Rodeo, *Pittier 5608*. Types (see Allen & Crosby 1986b). PC, holotype; G, H, isotypes.

Plants medium-sized to large, creeping or pendent, epiphytic. Primary stems to 35 cm long; stems in cross section with 4–6 rows of small, thick-walled, yellow to red epidermal cells, cortical cells enlarged, thin-walled, hyaline, central strand small. Secondary stems pendent, erect or becoming adnate to the substrate, identical to primary stems, irregularly or weakly pinnately branched, branches to 1.5 cm long. Stem and branch leaves weakly dimorphic, rarely trimorphic. Stem leaves erect-appressed, 2–4 × 1.0–1.8 mm, well spaced, laxly appressed, broadly ovate to deltoid, abruptly constricted to a long smooth or weakly serrulate hair-point, weakly cordate at base, strongly decurrent; margins entire, plane below, broadly incurved above. When trimorphic, stem leaves also ovate-lanceolate, erect to erect-patent, tortuose above, margins wavy and entire; costae single, weak; median cells linear-flexuose, 50–100 × 2.5–4.0 µm, firm-walled, porose or non-porose; alar cells strongly differentiated, reaching to and extending up the leaf margins, short-rectangular, lax and more or less inflated, hyaline at first, becoming orange red with age. Branch leaves erect to erect-spreading, 1.5–2.2 mm, broadly ovate to elliptic, somewhat rounded at base, long-acute to acuminate; margins entire below, irregularly denticulate above, plane or erect below, broadly inflexed above to just below the apices, apices more or less recurved; cells as in stem leaves. Dioicous. Setae yellow, becoming red with age, 0.7–0.9 mm long, smooth. Capsules immersed, erect, ellipsoid, 2.5–3.0 mm long; exothecial cells at the mouth quadrate to oblate, irregularly rectangular below, firm-walled; stomata on neck; opercula 1.5 mm long, shortly rostrate; annuli rudimentary, deciduous, of several rows of thick-walled cells; exostome teeth linear, lightly papillose; endostome lightly papillose, basal membranes 0.10–0.15 mm high, segments linear, cilia rudimentary or absent. Spores round to oblong, 20–33 µm, lightly papillose. Calyptrae mitrate, 1.8 mm long, densely hairy.

Illustrations. Allen and Crosby (1986b, Figs. 28–36); Buck (1998, Pl. 89 10–18). Figure 44.

Habitat. Epiphytic, usually pendent on tree trunks, branches, twigs, palm fronds, and leaves, also on rotting logs, occasionally on ground among grasses and on rocks along streams; 200–2000 m.

Distribution in Central America. BELIZE. Cayo: *Allen 15162* (BRH, MO); Toledo: *Allen 18973* (BRH, MO). GUATEMALA. Alta Verapaz: *Steyermark 44623a* (F); San Marcos: *Croat 40961B* (MO). HONDURAS. Francisco Morazán: *Standley 28289* (F, MO). NICARAGUA. Granada: *Stevens 4389* (MO); Matagalpa: *Stevens 9653a* (MO); Rivas: *Robleto 1123* (MO). COSTA RICA. Alajuela: *Lyon 626* (CR, MO); Cartago: *Griffin & Eakin 273* (FLAS); Guanacaste: *Bowers 430f* (MO); Puntarenas: *Liesner 17310* (CR, MO), Cocos Island: *Gómez 4596* (MO); San José: *Crosby & Crosby 6258* (CR, MO). PANAMA. Bocas del Toro: *Allen 5537* (MO); Chiriquí: *Cornman 3131* (F, FH, MO); Panamá: *Salazar 745* (MO); Veraguas: *Crosby 10155* (MO).

World range: Mexico; Central America; Caribbean; Western and Northern South America, Brazil.

Although *Squamidium isocladum* belongs to section *Squamidium*, it is gametophytically very close to *S. macrocarpum* of section *Macrosquamidium*. The species are similar in size, and they can be separated from all other *Squamidium* species by their branch leaves that are non-cordate at base, with extensively developed, more or less inflated and thin-walled alar cells, broad, long-acute to short-acuminate apices, and erect to shortly incurved upper leaf margins. *Squamidium macrocarpum* differs from *S. isocladum* in having stolon leaves with recurved marginal teeth, entire branch leaf margins, and

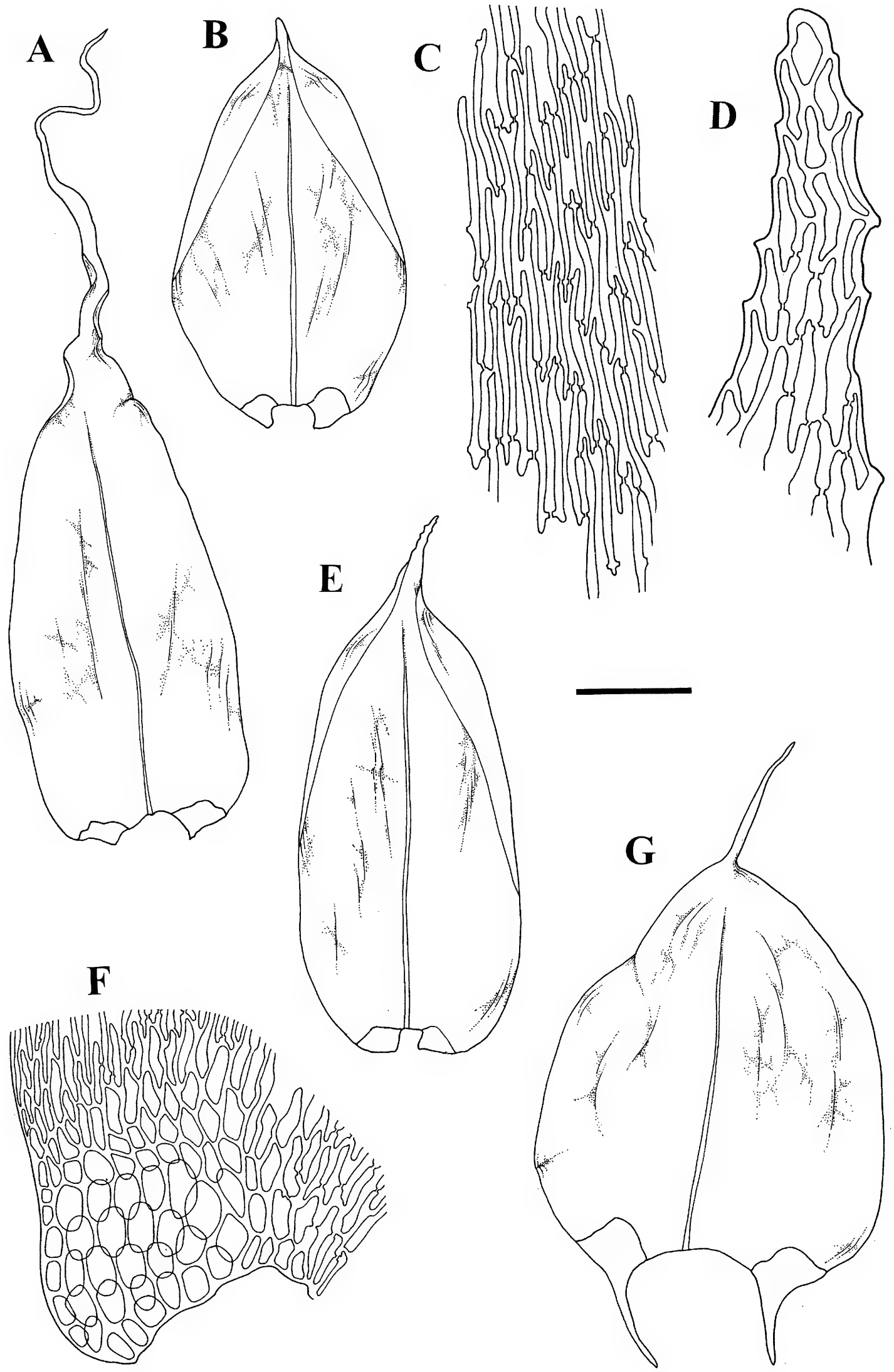


Figure 44. *Squamidium isocladum*. A. Stolon leaf. B & E. Branch leaves. C. Median leaf cells. D. Leaf apex. F. Alar cells. G. Stem leaf. Scale in mm: bar = 0.05 (C, D); bar = 0.06 (F); bar = 0.6 (A, B, E, G). All figure parts from *Crosby 2641*.

strongly galeate branch leaf apices. The best means of distinguishing *S. isocladum* from *S. macrocarpum* is the presence on its branch leaf apices of irregularly denticulate rather than entire margins.

The branch leaves of *Squamidium isocladum* are sometimes fairly long-pointed, and plants with this feature can be confused with *S. leucotrichum.* The two species are also similar in having weakly dimorphic stem leaves, loosely spreading branch leaves, and porose upper leaf cells. The branch leaves of *S. leucotrichum*, however, are consistently long- or hair-pointed, while those of *S. isocladum* usually have a mixture of long- and short-pointed leaves. Furthermore, *S. leucotrichum* has leaves with strongly cordate bases and alar cells restricted to the region below and interior to the cordate leaf bases. *Squamidium livens* is a smaller plant than *S. isocladum*, and it commonly has filiferous branches and strongly cordate leaf bases. The branch leaves of *S. livens* further differ from those of *S. isocladum* in having strongly galeate leaf apices and entire upper margins.

3. *Squamidium leucotrichum* (Taylor) Broth., Nat. Pflanzenfam. I(3): 809. 1906. *Hypnum leucotrichum* Taylor, London J. Bot. 7: 196. 1848. *Meteorium leucotrichum* (Taylor) Mitt., J. Linn. Soc., Bot. 12: 434. 1869. *Pilotrichella leucotricha* (Taylor) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 262. 1877. Protologue. [Ecuador] On Pichincha. *Prof. W. Jameson.* Feb. 1848. Types (see Allen & Crosby 1986b). FH, holotype; NY, isotype.

Plants medium-sized to large, creeping or pendent, corticolous or saxicolous. Primary stems to 35 cm long; stems in cross section with 2–5 rows of small, thick-walled, yellow to red epidermal cells, cortical cells enlarged, thin-walled, hyaline, central strand small. Secondary stems pendent, erect or becoming adnate to the substrate, identical to primary stems, irregularly or weakly pinnately branched, branches 1.0–2.5 cm long, at times elongating into stoloniferous branches to 4.0 cm long. Stem and branch leaves weakly dimorphic. Stem leaves erect-appressed, 2–4 × 0.5–1.5 mm, well spaced, laxly appressed, ovate-lanceolate to oblong, cordate at base, abruptly constricted to long, crispate, hair-points, strongly decurrent; margins entire or weakly serrulate; costae single, weak; median cells linear-flexuose, 62–125 × 4–6 µm, firm-walled, to incrassate; alar cells strongly differentiated, short-rectangular, thin-walled, inflated and bulging in excavate groups restricted to the region below and interior to the cordate bases, orange yellow, occasionally hyaline. Branch leaves spreading to erect-spreading, 1.5–4.5 mm long, broadly ovate to oblong from a cordate base, abruptly narrowed to long, crispate hair-points; margins entire below, inflexed and serrulate above; cells as in stem leaves. Dioicous. Setae yellow to yellow red, 1.0–1.2 mm long, smooth. Capsules immersed, erect, ellipsoid, 2.2–2.7 × 1.0–1.3 mm; exothecial cells at the mouth quadrate to oblate, irregularly rectangular below, firm-walled; stomata on neck; opercula 1.7–2.0 mm long, shortly rostrate; annuli rudimentary, deciduous, of several rows of thick-walled cells; exostome teeth linear, lightly papillose; endostome lightly papillose, basal membranes 0.10–0.17 mm high, segments linear, perforate, cilia rudimentary or absent. Spores round to oblong, 15–33 µm, lightly papillose. Calyptrae mitrate, 2.0–2.5 mm long, densely hairy.

Illustrations. Bartram (1949, Fig. 117 F–G); Florschütz (1964, Fig. 102 a–g); Allen and Crosby (1986b, Figs. 8–20); Sharp *et al.* (1994, Fig. 539 h–i, Fig. 540); Churchill (1994, Fig. 27 A); Churchill and Linares (1995, Fig. 126 e–h); Duarte Bello (1997, Pl. 204); Buck (1998, Pl. 88 1–6); Buck (2003, Fig. 127). Figure 45.

Habitat. Epiphytic, often pendent on tree trunks, branches, twigs, and leaves, occasionally on soil banks or rocks and boulders in woods; 140–3000 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: *Türckheim 7141* (FH, H); Baja Verapaz: *Sharp 5164* (F); Chiquimula: *Steyermark 31439* (F, FH); Guatemala: *Standley 58459a* (F, FH); Huehuetenango: *Steyermark 49763c* (F). HONDURAS. Atlántida: *Allen 17371* (MO, TEFH); Comayagua: *Allen 13750* (MO, TEFH); Cortés: *Allen 14100* (MO, TEFH); Lempira: *Allen 11910* (MO, TEFH); Francisco Morazán: *Williams et al. 42866* (MO); Ocotepeque: *Allen 14474* (MO, TEFH); Olancho: *Allen 12615* (MO, TEFH); Santa Bárbara: *Allen 11601* (MO, TEFH). NICARAGUA. Estelí: *Stevens 16234B* (MO); Granada: *Miller 1428A* (MO); Jinotega: *Stevens 1131* (HNMN, MO); Matagalpa: *Gladstone & Hruska 2184B* (MO). COSTA RICA. Alajuela: *Brenes 17071* (F, FH); Cartago: *Crosby & Crosby 6180* (CR, MO); Heredia: *Crosby & Crosby 8647* (MO); Limón: *Gutiérrez 193* (CR, F); Puntarenas: *Crosby 9948* (MO); San José: *Crosby & Crosby 6231* (CR, MO).

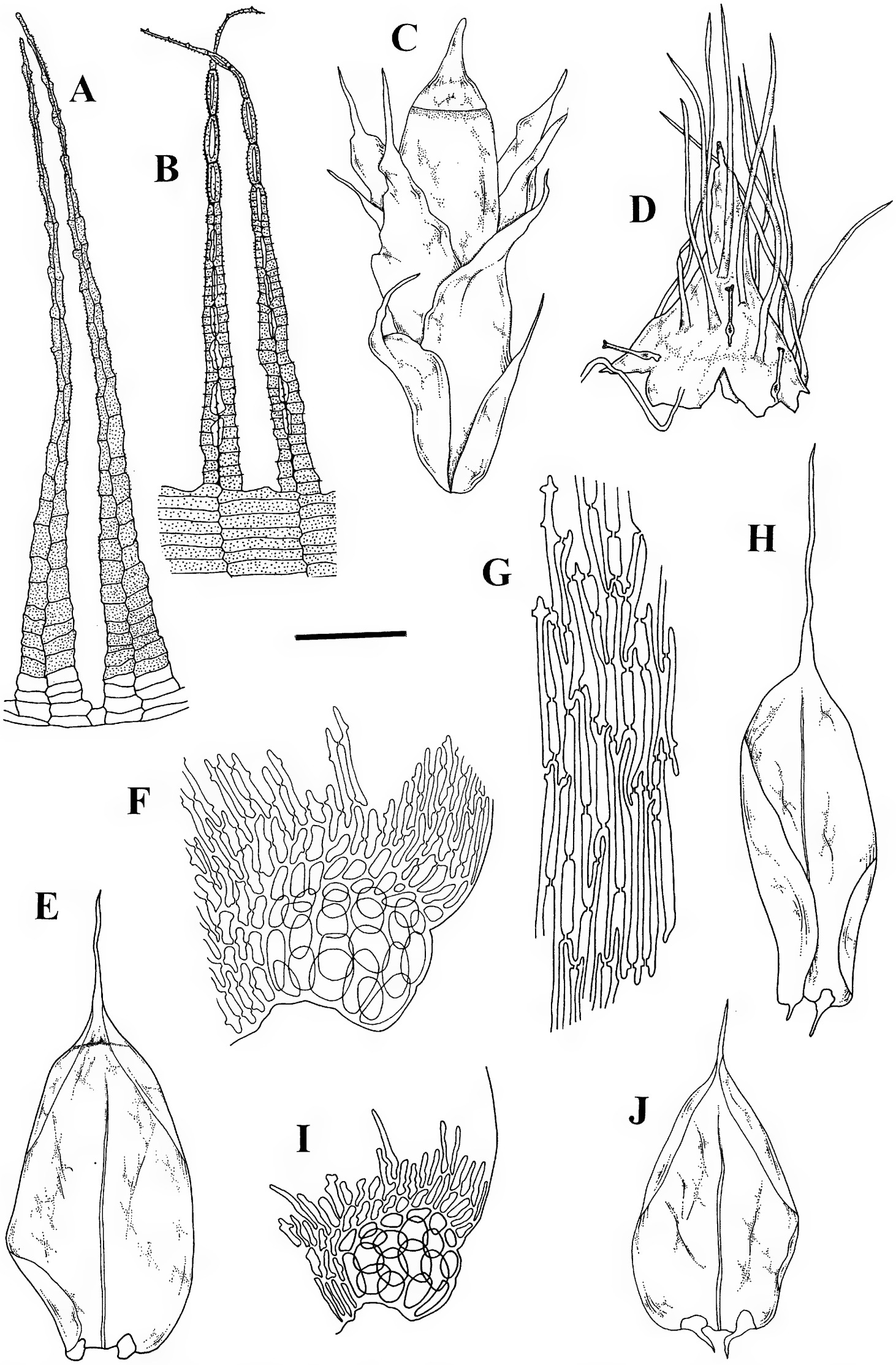
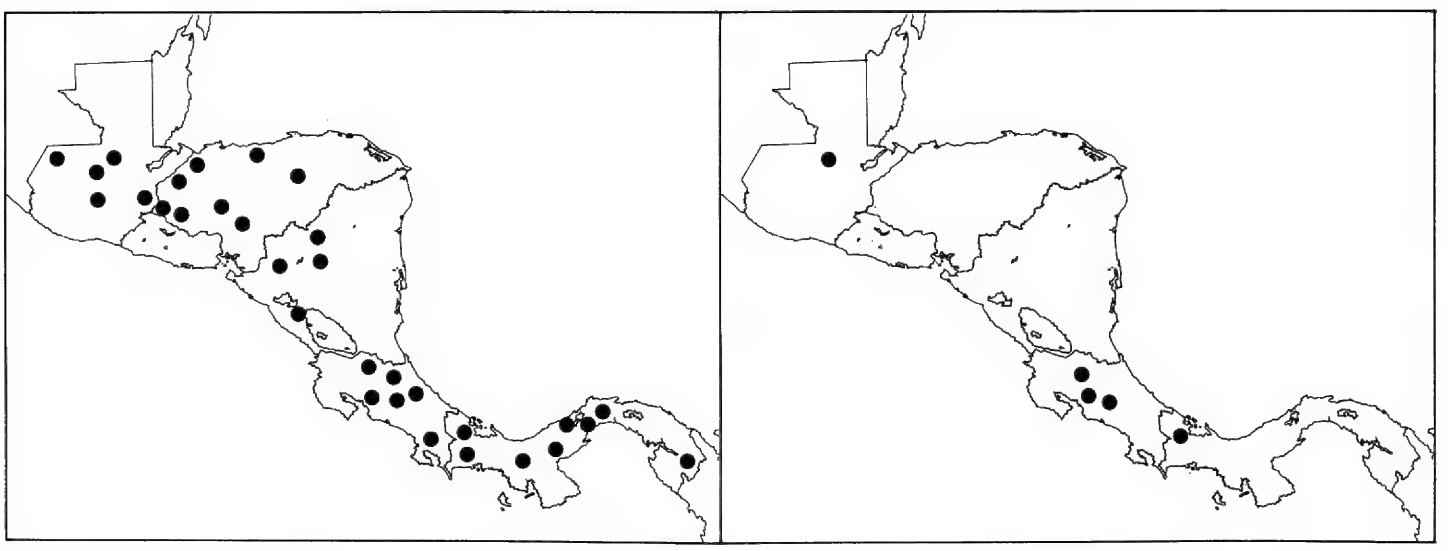


Figure 45. *Squamidium leucotrichum*. A. Exostome, dorsal (outer) surface. B. Endostome, dorsal (outer) surface. C. Seta, capsule, and operculum. D. Calyptra. E. Stem leaf. F & I. Alar cells. G. Median leaf cells. H. Stolon leaf. J. Branch leaf. Scale in mm: bar = 0.05 (A, B, G); bar = 0.06 (F, I); bar = 0.4 (C); bar = 0.6 (E, H, J); bar = 1.2 (D). All figure parts from *Crosby & Crosby 6341*.



Squamidium leucotrichum *Squamidium livens*

PANAMA. Bocas del Toro: *Allen 5695* (MO, PMA); Canal Area: *Porter et al. 4991A* (MO); Chiriquí: *Allen 5397* (MO, PMA); Coclé: *Dwyer & Correa 8861* (MO); Colón: *Crosby 10707* (MO); Darién: *Allen 8905* (MO, PMA); Panamá: *Crosby 10041* (MO); Veraguas: *Crosby 10274* (MO).

World range: Mexico; Central America; Caribbean; Western and Northern South America, Brazil.

Squamidium leucotrichum is gametophytically characterized by its loosely spreading, long-acuminate to hair-pointed leaves that are cordate to strongly rounded at the insertion and have bulging, thin-walled alar cells restricted to small, excavate groups below the cordate leaf bases. It is the only Central American species of *Squamidium* with consistently narrowly acuminate to hair-pointed leaves.

The branch leaves of *S. livens* are similar to those of *S. leucotrichum* in having cordate bases, and both species have bulging, thin-walled alar cells restricted to small excavate groups. In addition, both species sometimes have filiform branches, although this feature is much more common in *S. livens* than in *S. leucotrichum*. *Squamidium livens* differs from *S. leucotrichum* in having broadly acuminate to acute, often galeate leaf apices. *Squamidium macrocarpum* and *S. isocladum* are similar in size to *S. leucotrichum*, and all three species have laxly erect to spreading branch leaves with lax, thin-walled, more or less bulging alar cells. In *S. macrocarpum* and *S. isocladum*, however, the branch leaves are rounded rather than cordate at base, and they have mostly short-acuminate to acute apices. *Squamidium isocladum* also differs from *S. leucotrichum* in having branch leaves with irregularly denticulate upper leaf margins. *Squamidium macrocarpum* further differs from *S. leucotrichum* in having exserted capsules and stolon leaves with recurved marginal teeth extending from the leaf apex to the shoulders.

4. *Squamidium livens* (Schwägr.) Broth., Nat. Pflanzenfam. (ed. 2) 11: 157. 1925. *Hypnum livens* Schwägr., Sp. Musc. Frond. Suppl. 1(2): 211. 1816. *Isothecium livens* (Schwägr.) Brid., Bryol. Univ. 2: 380. 1827. *Neckera livens* (Schwägr.) Müll. Hal., Syn. Musc. 2: 128. 1850. *Meteorium livens* (Schwägr.) Mitt., J. Linn. Soc., Bot. 12: 433. 1869. *Pilotrichella livens* (Schwägr.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 258. 1877. Protologue. In Peruvia lectum conservat *Jussieuus*. Type (see Allen & Crosby 1986b). G, lectotype.

Pilotrichum filiferum Müll. Hal., Bot. Zeitung (Berlin) 6: 767. 1848. *Neckera filifera* (Müll. Hal.) Müll. Hal., Syn. Musc. 2: 133. 1850. *Meteorium filiferum* (Müll. Hal.) Mitt., J. Linn. Soc., Bot. 12: 434. 1869. *Pilotrichella filifera* (Müll. Hal.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 261. 1877. *Squamidium filiferum* (Müll. Hal.) Broth., Nat. Pflanzenfam. I(3): 808. 1906. Protologue. Venezuela, prov. Mérida, Lagunetta bei Mérida, 6500 ft., September 1846, ad arboris *Funk & Schlim. 991*. Types (see Allen & Crosby 1986b). H, lectotype; BM, JE, isolectotypes.

Plants small to medium-sized, creeping or pendent, corticolous. Primary stems to 15 cm long; stems in cross section with 2–5 rows of small, thick-walled, yellow to red epidermal cells, cortical

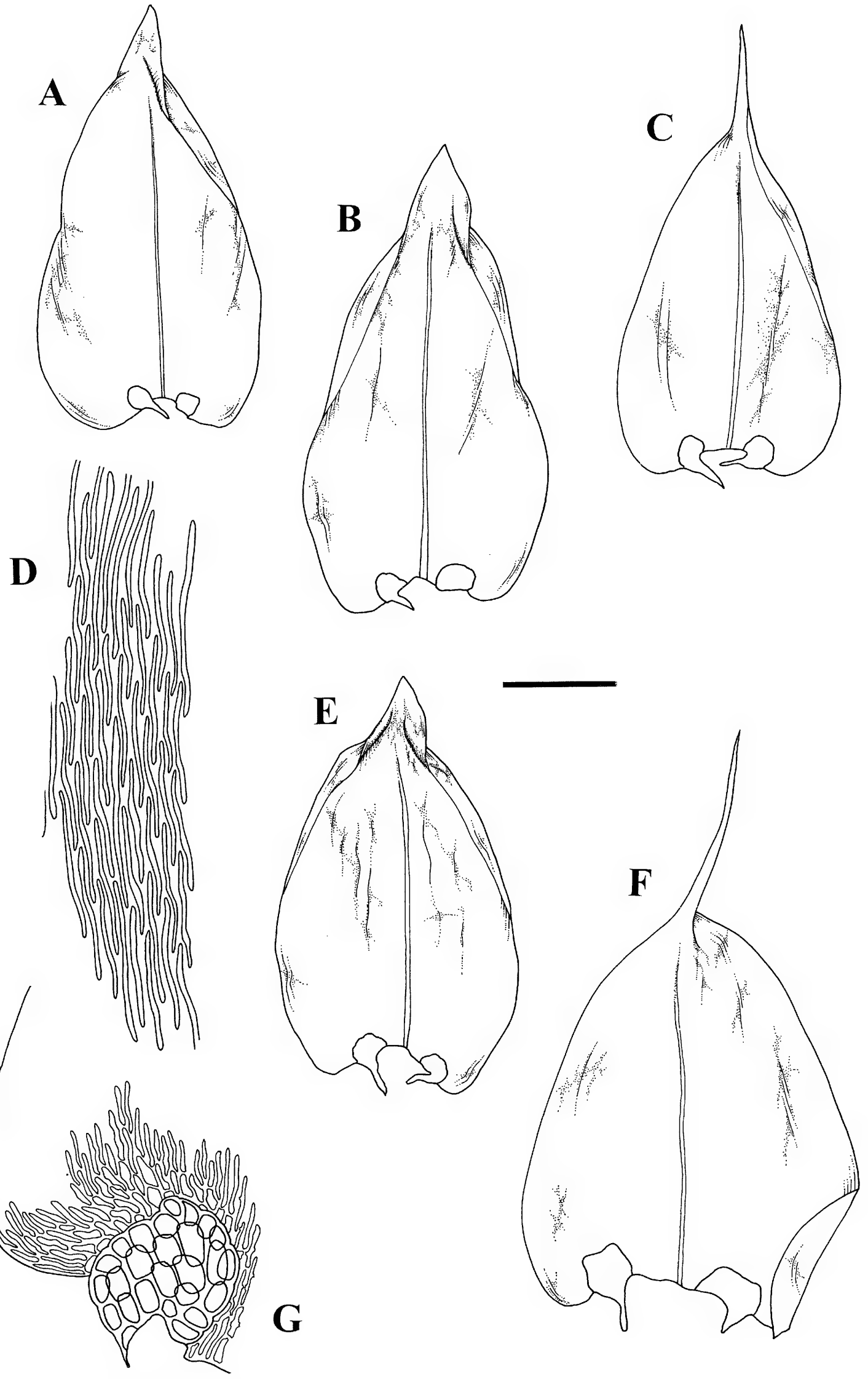


Figure 46. *Squamidium livens*. A, B & E. Branch leaves. C. Stem leaf. D. Median leaf cells. F. Stolon leaf. G. Alar cells. Scale in mm: bar = 0.06 (D, G); bar = 0.6 (A–C, E, F). All figure parts from *Crosby & Crosby 6253*.

cells enlarged, thin-walled, hyaline, central strand small (occasionally absent). Secondary stems pendent, erect or becoming adnate to the substrate, identical to primary stems. Primary branches 1.0–2.5 cm long, occurring singly or in well-separated, fasciculate groups of 2–4, at times elongating into filiferous branches. Filiferous branches nearly always present on stems, to 10 cm long. Leaves dimorphic: stem and filiferous branch leaves of one type, primary branch leaves of another. Stem leaves erect to erect-spreading when moist, appressed when dry, 1.5–3.5 × 0.9–1.8 mm, well spaced, broadly ovate to oblong, cordate at base, abruptly setaceous into long acumina, strongly decurrent; margins entire; costae single, weak; median cells linear-flexuose, 42–112 × 4–7 µm, firm-walled, not porose; alar cells strongly differentiated, short-rectangular, thin-walled, inflated and bulging in excavate groups restricted to the region below and interior to the cordate bases, reddish yellow to hyaline. Branch leaves 0.8–2.2 mm long, broadly ovate with acute to rounded acute apices; margins plane below, broadly inflexed above to just below the apex, then abruptly plane and forming a galeate apex, entire or minutely serrulate above; cells as in stem leaves. Dioicous. Setae red, 0.2 mm long, smooth. Capsules immersed, erect, ellipsoid, 2.5 × 1.5 mm; exothecial cells quadrate to oblate at the mouth, irregularly rectangular below, firm-walled; stomata on neck; opercula 1.2 mm long, shortly rostrate; annuli rudimentary, deciduous, of several rows of thick-walled cells; exostome teeth linear, smooth below, lightly papillose above; endostome smooth below, lightly papillose above, basal membranes 0.12–0.15 mm high, segments linear, perforate, cilia rudimentary or absent. Spores round, 17–23 µm, lightly papillose. Calyptrae mitrate, 2.0 mm long, lightly hairy.

Illustrations. Allen and Crosby (1986b, Figs. 21–27); Churchill and Linares (1995, Fig. 127 i–m); Buck (1998, Pl. 89 1–9). Figure 46.

Habitat. Epiphytic, often pendent on tree trunks, branches, twigs, and fern stipes, occasionally on rotten logs; 700–2450 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: *Standley 71070* (F, FH). COSTA RICA. Alajuela: *Stevens 13838* (MO); Cartago: *Crosby & Crosby 6335* (CR, MO); San José: *Crosby & Crosby 6240* (CR, MO). PANAMA. Bocas del Toro: *Allen 5270* (MO, PMA).

World range: Central America; Caribbean; Western and Northern South America.

Squamidium livens is a medium-sized plant that commonly has numerous long, filiferous branches. It has immersed capsules and stolon leaves with entire margins. The branch leaves in *S. livens* are strongly cordate at base, with thin-walled, inflated alar cells more or less restricted to the region below the cordate leaf base and galeate leaf apices with entire margins. *Squamidium leucotrichum* sometimes has filiferous branches, and its branch leaves have cordate bases as well as alar cells similar to those of *S. livens*. It differs from *S. livens* in having long-acuminate to piliferous branch leaves that are never galeate at the apex.

Squamidium nigricans and *S. livens* are similar in size, and in both species the branch leaves are acute to shortly apiculate. Plants of *S. nigricans*, however, never have filiferous branches. Furthermore, the branch leaves in *S. nigricans* are not galeate at the apex; they are at best rounded to the insertion, and have more extensively developed alar cells. Galeate branch leaf apices are found in both *S. macrocarpum* and *S. livens*. However, *S. macrocarpum* is a larger plant than *S. livens*, with branch leaves rounded to the insertion, exserted capsules, and sharply recurved teeth on the upper margins of the stolon leaves. Plants of *S. isocladum* are larger than those of *S. livens*, and, furthermore, their branch leaves are rounded to the insertion and have non-galeate, irregularly denticulate apices.

5. *Squamidium macrocarpum* (Spruce *ex* Mitt.) Broth., Nat. Pflanzenfam. I(3): 809. 1906. *Meteorium macrocarpum* Spruce *ex* Mitt., J. Linn. Soc., Bot. 12: 437. 1869. Protologue. Andes Peruvianae, in monte Guayrapurina, ad ramulos Artocarpae cujusdam (vel potium Lacistemae), socio M. flaccido, *Spruce 1191 & 1194*. Types (see Allen & Crosby 1986b). *Spruce 1191*, *1194* (NY, lectotype [one specimen with two numbers]; BM, syntypes).

Squamidium crispipilum E. B. Bartram, J. Wash. Acad. Sci. 24: 475. 1934. Protologue. Costa Rica. Two miles southwest of Agua Caliente, 1050 m, April 1 1928, *Stork 1338*. Types (see Allen & Crosby 1986b). FH, holotype; G, isotype.

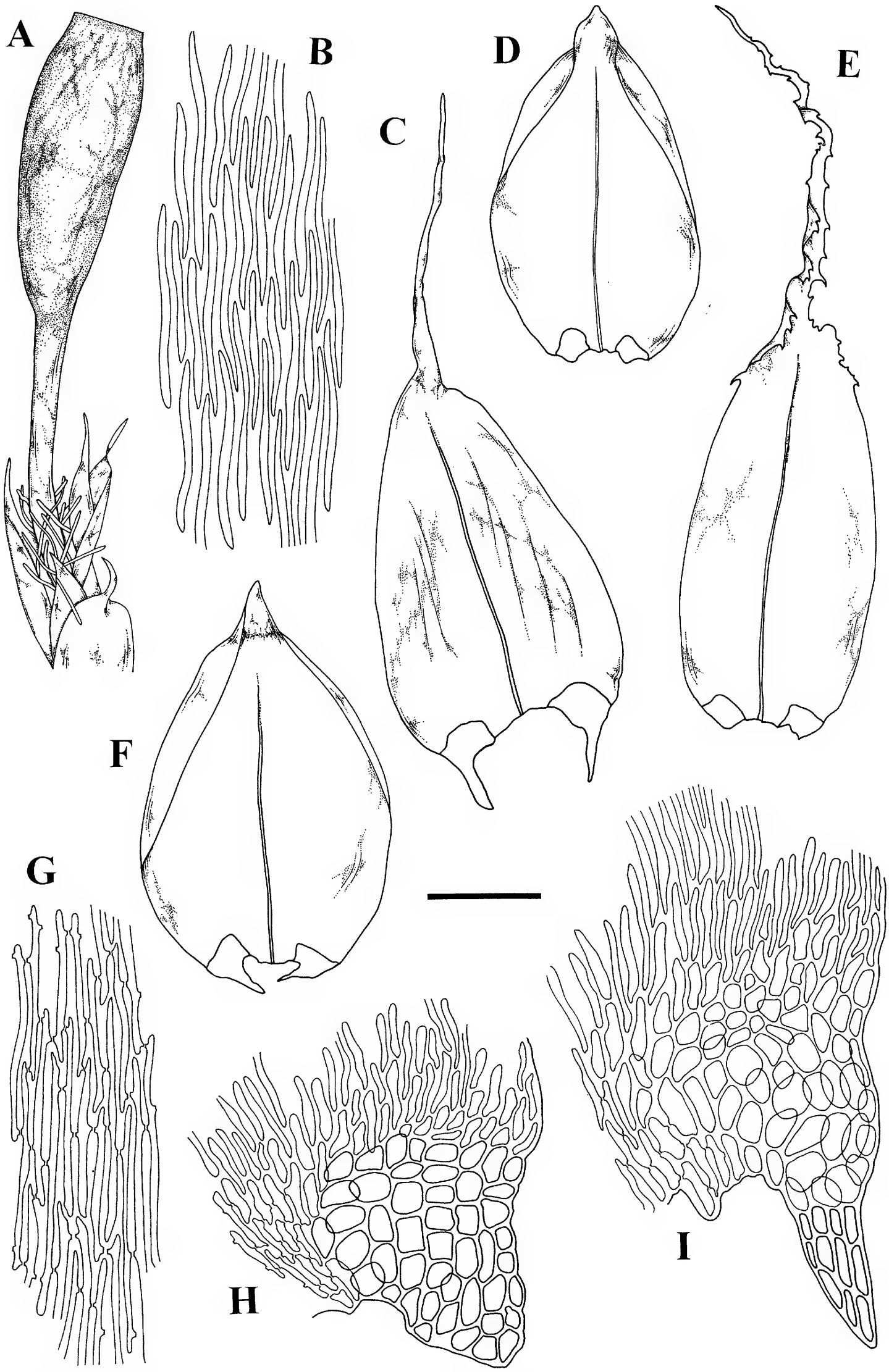
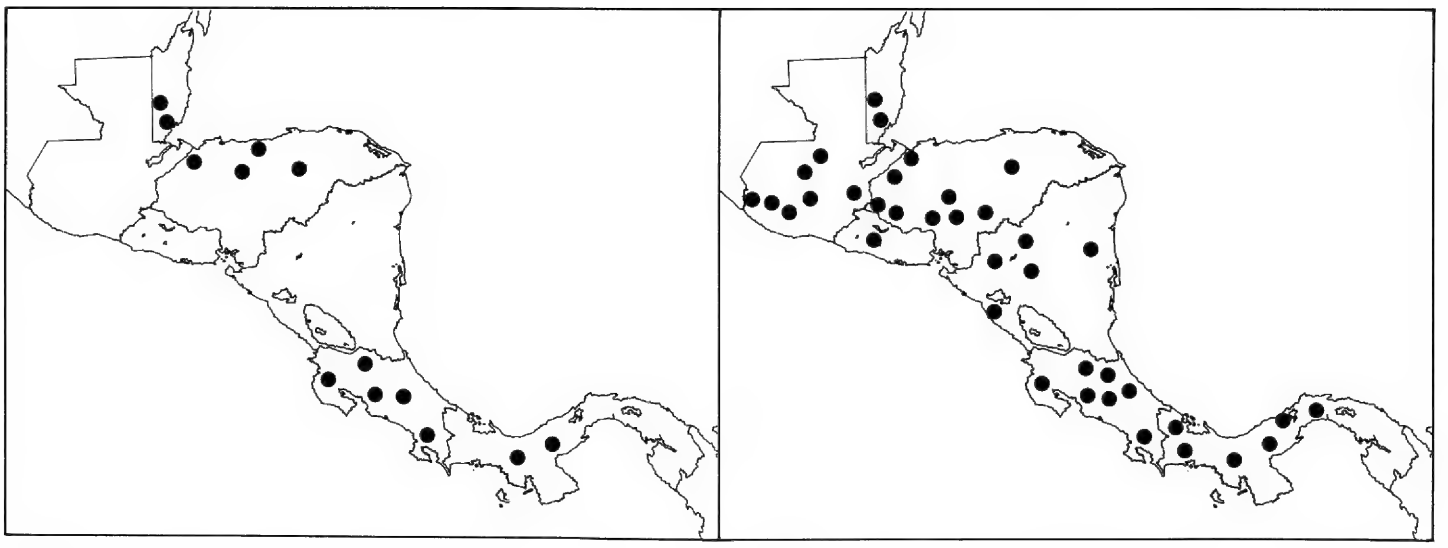


Figure 47. *Squamidium macrocarpum*. A. Seta and capsule. B & G. Median leaf cells. C. Stem leaf. D & F. Branch leaves. E. Stolon leaf. H & I. Alar cells. Scale in mm: bar = 0.06 (B, G, H, I); bar = 0.6 (C–E, F); bar = 1.0 (A). All figure parts from *Crosby 6258*.



Squamidium macrocarpum *Squamidium nigricans*

Plants medium-sized, creeping or pendent, epiphytic. Primary stems to 30 cm long; stems in cross section with 2–3 rows of small, thick-walled, yellow to red epidermal cells, cortical cells enlarged, thin-walled, hyaline, central strand small. Secondary stems pendent, erect or becoming adnate to the substrate, identical to primary stems, irregularly or densely branched, branches to 1.5 cm long, at times elongating into flagella. Leaves trimorphic: stolon leaves, primary stem leaves, and branch leaves. Stolon leaves 3–4 × 0.5–1.5 mm, erect to erect-patent, ovate-lanceolate, tortuose above; margins dentate with recurved teeth from the shoulders to apex. Primary stem leaves erect-appressed, similar in size to stolon leaves, broadly ovate below, abruptly acuminate above, strongly decurrent; margins entire or weakly serrulate above; costae single, weak; median cells linear flexuose, 55–105 × 4–5 µm, firm-walled, occasionally porose; alar cells strongly differentiated, short- to long-rectangular, more or less bulging, at times firm-walled. Branch leaves erect to erect-spreading, at times loosely tumid, frequently in seriate rows, 1–2 × 0.5–1.0 mm, broadly ovate to elliptic, shortly acute to rounded-acute, galeate; margins entire and plane below, erect to incurved, serrulate above. Dioicous. Setae yellow red to dark red, 2–3 mm long, smooth. Capsules exserted, erect, ellipsoid, 2.0–2.7 mm long, exothecial cells quadrate to oblate at mouth, irregularly rectangular below, firm-walled; stomata on neck; opercula 1.0–1.5 mm long, shortly rostrate; annuli rudimentary, deciduous, of several rows of thick-walled cells; exostome teeth linear, papillose throughout or papillose above and smooth below; endostome lightly papillose, basal membranes 0.13–0.14 mm high, segments linear, not perforate, cilia rudimentary or absent. Spores round, 17–32 µm, lightly papillose. Calyptrae mitrate, 3 mm long, densely hairy.

Illustrations. Crosby (1971, Figs. 4–8); Allen and Crosby (1986b, Figs. 59–72); Churchill and Linares (1995, Fig. 127 a–d). Figure 47.

Habitat. Epiphytic, on trunks, branches, vines, and twigs of trees and shrubs; 500–1800 m.

Distribution in Central America. BELIZE. Cayo: *Croat* 23756 (MO); Toledo: *Allen* 18646 (BRH, MO). HONDURAS. Atlántida: *Allen 17465* (MO, TEFH); Cortés: *Morton 7636b* (US); Olancho: *Allen 12788* (MO, TEFH); Yoro: *Allen 13650* (MO, TEFH). COSTA RICA. Alajuela: *Crosby 3755* (MO); Cartago: *Standley 33611b* (F, FH); Guanacaste: *Dodge et al. 6694* (FH); Puntarenas: *Crosby 2706* (MO); San José: *Crosby & Crosby 6258* (MO). PANAMA. Coclé: *Croat 25297* (MO); Veraguas: *Crosby 10155* (MO).

World range: Central America; Western, Northern, and Southern South America, Brazil.

Squamidium macrocarpum is a medium-sized species with erect to erect-spreading, loosely tumid branch leaves that are often in seriate rows. The branch leaves have galeate apices and thin-walled, bulging, shortly rectangular alar cells. It belongs to section *Macrosquamidium*; the only other member of that section, *S. diversicoma*, is smaller in size and has imbricate branch leaves when dry, cuspidate apices, and thick-walled, firm, quadrate to oblate alar cells.

When sporophytes and stolon leaves are absent, *S. macrocarpum* is difficult to distinguish from *S. isocladum*. Both species are similar in size and can be separated from all other *Squamidium* species by their branch leaves that are non-cordate at base and have extensively developed, more or less inflated and thin-walled alar cells, broad, long-acute to short-acuminate apices, and erect to shortly incurved upper margins. In the absence of sporophytes and stolon leaves, *S. isocladum* differs from *S. macrocarpum* only in having branch leaves with non-galeate apices and irregularly denticulate margins. *Squamidium livens* is similar to *S. macrocarpum* in having galeate branch leaf apices. It is, however, a smaller plant than *S. macrocarpum*; it commonly has numerous flagellate branches; and its non-seriate branch leaves are cordate at base.

6. *Squamidium nigricans* (Hook.) Broth., Nat. Pflanzenfam. I(3): 808. 1906. *Hypnum nigricans* Hook. *in* Kunth, Syn. Pl. 1: 64. 1822. *Isothecium nigricans* (Hook.) Brid., Bryol. Univ. 2: 363. 1827. *Neckera nigricans* (Hook.) Nees, Linnaea 19: 682. 1847. *Meteorium nigricans* (Hook.) Mitt., J. Linn. Soc., Bot. 12: 433. 1869. *Pilotrichum nigricans* (Hook.) Hampe, Bot. Zeitung (Berlin) 27: 450. 1869. *Pilotrichella nigricans* (Hook.) Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 223. 1872. Protologue. [Colombia] Crescit in sylvis inter pasto et Teindala, alt. 1360 hex. (Provincia de los Pastos). *Humboldt & Bonpland*. Types (see Allen & Crosby 1986b). BM, holotype; BM, G, NY, S, isotypes.

Pilotrichella tenuinervis Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32(1): 181. 1894. *Squamidium tenuinerve* (Renauld & Cardot) Broth. *ex* Paris, Coll. Nom. Broth. 31. 1909. Protologue. [Costa Rica] Général (*Pittier n° 5607*). Forêts du Rio Naranjo, 200–250 m. (*n^os 5683*, *5684*, *5686*). San Marcos de Dota (*n°5685*). Types (see Allen & Crosby 1986b). *Pittier 5684* (PC, lectotype; H, isolectotype); *Pittier 5683* (G, H, syntypes).

Orthostichella anacamptacea Müll. Hal. *in* Broth., Nat. Pflanzenfam. I(3): 808. 1906, invalid name, lacks a description. Based on: Guatemala, leg. *Sarg. no. 5* (H).

Plants small to medium-sized, creeping or pendent, corticolous or saxicolous. Primary stems to 45 cm long; stems in cross section with 2–5 rows of small, thick-walled, yellow to red epidermal cells, cortical cells enlarged, thin-walled, hyaline, central strand small (occasionally absent). Secondary stems pendent, erect or becoming adnate to the substrate, identical to primary stems. Primary branches to 0.5–2.0 cm long, occurring singly or in well-separated, fasciculate groups of 2–4. Stem and branch leaves weakly dimorphic. Stem leaves 1.0–2.0 × 0.7–1.2 mm, laxly appressed, well spaced, broadly ovate, occasionally deltoid, not or weakly cordate at base, abruptly constricted to long apiculi or hair-points, strongly decurrent; margins entire or serrulate, plane or incurved above; costae single, weak; median cells linear-flexuose, 32–100 × 2.5–4.0 µm, firm-walled, not or rarely incrassate; alar cells strongly differentiated, short-rectangular to quadrate, in bulging excavate groups, orange yellow to hyaline. Branch leaves 0.6–1.7 mm long, loosely imbricate to erect-spreading, sometimes in distinct spiral rows, broadly oblong-ovate, abruptly apiculate to short-acute, apices recurved; margins plane below, broadly inflexed above, serrulate above; cells as in stem leaves. Dioicous. Setae red, 0.2–0.3 mm long, smooth. Capsules immersed, erect, ellipsoid, 2.0–2.5 × 1.3 mm; exothecial cells quadrate to oblate at the mouth, irregularly rectangular below, firm-walled; stomata on neck; opercula 1.5 mm long, shortly rostrate; annuli rudimentary, deciduous, of several rows of thick-walled cells; exostome teeth linear, smooth below, lightly papillose above; endostome lightly papillose throughout, basal membranes 0.12–0.15 mm high, segments linear, not or sometimes narrowly perforate, cilia absent. Spores round to oblong, 15–35 µm, lightly papillose. Calyptrae mitrate, 1.7–1.8 mm, long, lightly hairy.

Illustrations. Dozy and Molkenboer (1854, Pl. 12 1–21); Brotherus (1906c, Fig. 604 A–F); Brotherus (1925, Fig. 550 A–F); Bartram (1949, Fig. 117 D–E); Allen and Crosby (1986b, Figs. 37–46); Sharp *et al.* (1994, Figs. 538 & 539 a–d); Churchill (1994, Fig. 27 B); Churchill and Linares (1995, Fig. 127 e–h); Duarte Bello (1997, Pl. 205); Buck (1998, Pl. 88 7–12). Figure 48.

Habitat. Epiphytic on tree and shrub trunks, branches, twigs, and leaves, also on vines, occasionally on rocks in woods and terrestrial on road banks; 150–2100 m.

Distribution in Central America. BELIZE. Cayo: *Allen 15161* (BRH, MO); Toledo: *Allen 18705* (BRH, MO). GUATEMALA. Alta Verapaz: *Standley 90398* (F, FH, NY, S, US); Baja Verapaz: *Stan-*

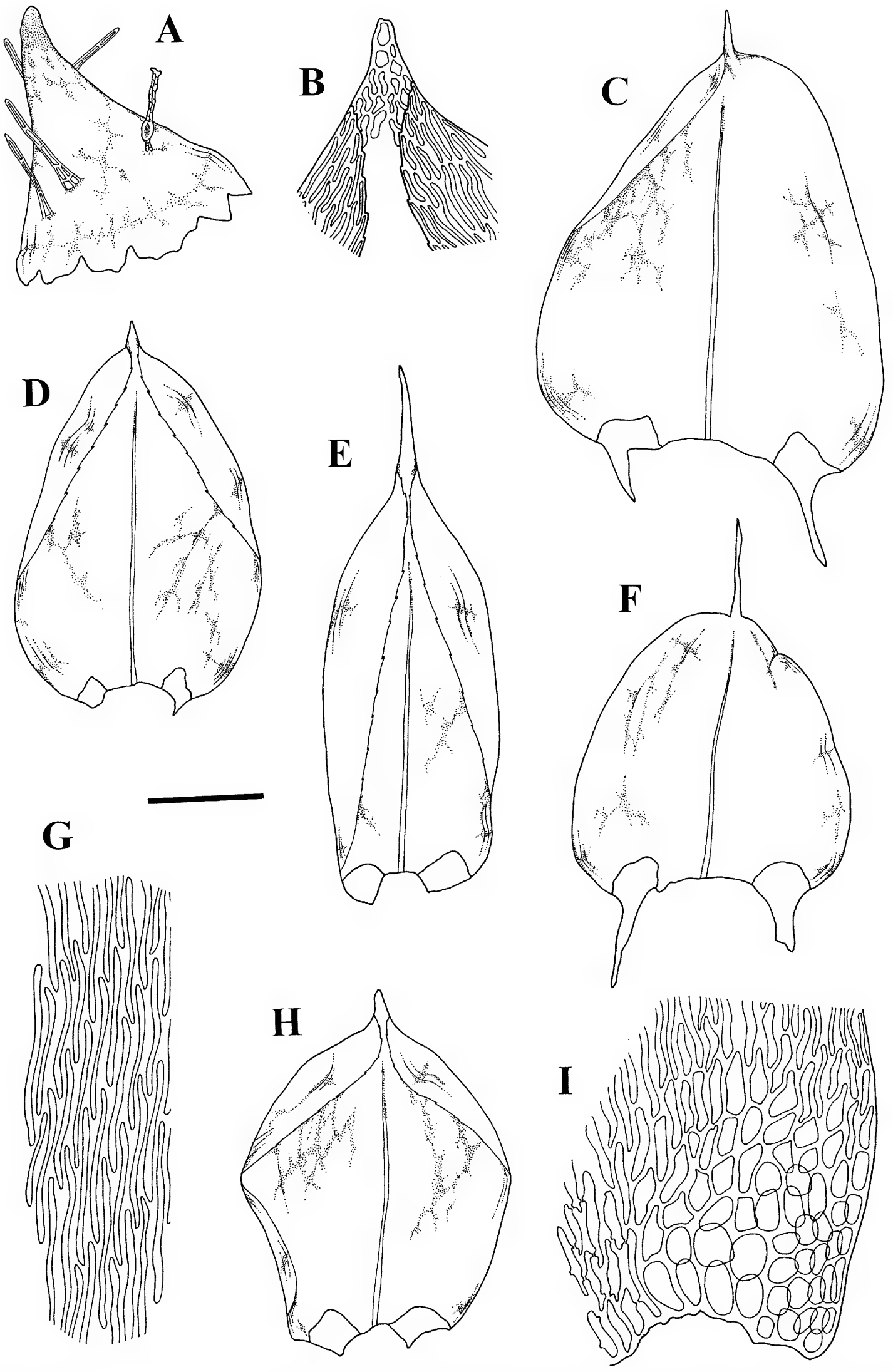


Figure 48. *Squamidium nigricans*. A. Calyptra. B. Leaf apex. C & E. Stem leaves. D & H. Branch leaves. F. Stolon leaf. G. Median leaf cells. I. Alar cells. Scale in mm: bar = 0.05 (G); bar = 0.06 (I); bar = 0.15 (B); bar = 0.6 (C–F, H); bar = 0.72 (A). All figure parts from *Crosby 4402*.

dley 69917 (F, FH); Chiquimula: *Steyermark 30600* (F, FH, NY, S); Guatemala: *Standley 58415b* (FH); Quetzaltenango: *Standley 85511b* (F, FH); San Marcos: *Standley 68922* (F, FH); Sololá: *Kellerman* (DUKE, U, US). EL SALVADOR. San Salvador: *Carlson 429a* (FH). HONDURAS. Comayagua: *Allen 13722* (MO, TEFH); Cortés: *Allen 14363* (MO, TEFH); El Paraíso: *Valerio R. 1768* (FH, MO); Francisco Morazán: *Allen 123872* (MO, TEFH); La Paz: *Allen 14555* (MO, TEFH); Lempira: *Allen 11096* (MO, TEFH); Ocotepeque: *Allen 14428* (MO, TEFH); Olancho: *Allen 12793B* (MO); Santa Bárbara: *Allen 11813* (MO, TEFH). NICARAGUA. Estelí: *Moreno 11124* (MO); Jinotega: *Stevens 43108* (HNMN, MO); Managua: *Standley 8204* (F, MO); Matagalpa: *Almedo 1451b* (MO); Zelaya: *Stevens 4900* (HNMN, MO). COSTA RICA. Alajuela: *Brenes 1182a* (MO, NY); Cartago: *Griffin 019968* (MO); Guanacaste: *Standley 45520* (FH, NY, US); Heredia: *Koch 4933* (MO); Limón: *Standley & Valerio 48695* (FH, NY, US); Puntarenas: *Lyon 288* (CR, MO); San José: *Standley & Valerio 51832* (FH, H, JE, NY, US). PANAMA. Bocas del Toro: *Allen 5280A* (MO, PMA); Chiriquí: *Killip 5254* (F, US); Coclé: *Crosby 4402* (MO, PMA); Colón: *Crosby 10348* (MO, PMA); Panamá: *Crosby 4375* (MO, PMA); Veraguas: *Crosby 10265* (MO, PMA).

World range: Mexico; Central America; Caribbean; Western and Northern South America.

Squamidium nigricans is a small to medium-sized species, with weakly dimorphic stem and branch leaves. In most collections there is complete intergradation between stem and branch leaves, with many stems having typical branch leaves. *Squamidium leucotrichum* is the only other species in the genus with such weakly dimorphic leaves. It differs from *S. nigricans* in having hair-pointed to long-acuminate leaves. The branch leaves in *S. nigricans* are apiculate to shortly acute, with broadly incurved, serrulate upper margins. The costae in *S. nigricans* are often exceptionally faint, and the dry branch leaves are usually arranged in seriate rows. The branch leaf costae in *S. nigricans* can be so weakly expressed that without careful examination they are not observed, causing it to be confused with the ecostate *Pilotrichella flexilis*. The two species are also similar in having branch leaves with strongly incurved upper margins and recurved apices. *Pilotrichella flexilis* differs from *S. nigricans* in its considerably larger size, much better developed, often reddish orange alar cells, branch leaves not in seriate rows, and exserted capsules. Although most *Squamidium* species have variously serrulate leaf margins, only *S. nigricans* has branch leaf margins that are consistently, evenly serrulate and so incurved that they nearly touch each other just below the apices. Other branch leaf features that help in recognizing the species include its thin-walled, lax, and bulging alar cells and leaf bases that are more or less straight to the insertions. Some forms of *S. nigricans* can be difficult to distinguish from *S. macrocarpum* and *S. isocladum*, because all three species have short-pointed branch leaves, lax, thin-walled alar cells, and branch leaves at times arranged in distinct seriate rows. *Squamidium macrocarpum* and *S. isocladum* are more robust plants than *S. nigricans*, with hair-pointed stem leaves (the former has stolon leaves with recurved marginal teeth), and with branch leaves that are not broadly incurved below the apex (both may have galeate branch leaf apices).

8. *Toloxis* W. R. Buck, Bryologist 97: 436. 1994.

Loxotis W. R. Buck, J. Hattori Bot. Lab. 75: 59. 1994, illegitimate homonym, not *Loxotis* R. Br. *ex* Benth., Scroph. Ind. 57. 1835.

Plants slender, medium-sized, or robust, green, yellow green, or yellow brown, often blackish with age, in mats or pendent masses. Stems pendent or creeping, irregularly or regularly pinnately branched; stems in cross section with sclerodermis, enlarged, thick-walled cortical cells, and small central strand; paraphyllia absent; pseudoparaphyllia foliose; rhizoids sparse, present only where stems or branches touch the substrate, brown, smooth, not branched, from circular clusters of initials abaxial to the leaf insertions. Stem and branch leaves differing only in size, erect, somewhat incurved when dry, erect-spreading when wet, slender, lanceolate-triangular, inserted in a U-shaped line, weakly plicate, erect-clasping at base, gradually acuminate, apices twisted when wet or dry, auriculate, auricles undulate, not decurrent; margins plane, serrate throughout, at times dentate on the auricles; costae single, ending at or just above midleaf, in cross section cells homogeneous; upper and median cells densely seriate-pluripapillose over cell lumina, elongate to fusiform, thick-walled, porose, extreme basal cells elongate, porose, smooth; alar cells poorly developed, irregularly quadrate

or subrectangular, lightly papillose, thick-walled, porose. Dioicous. Sporophyte not seen, description from Noguchi (1976) and Buck (1998). Setae short, 1–2 mm long, somewhat scabrous. Capsules erect, oblong; exothecial cells subquadrate to short-rectangular, firm-walled, evenly thickened; operc ula obliquely rostrate; exostome teeth yellow, linear-triangular, indistinctly papillose; endostome basal membranes high, segments linear, keeled and perforate, cilia absent. Spores papillose. Calyptrae cucullate, naked.

Toloxis is a genus of three species (Buck 1994a): one in the Neotropics, one in Madagascar, and one in tropical Asia. The genus grows predominantly pendent from tree trunks, branches, and twigs. Central American plants of *Toloxis* are slender to medium-sized, with irregularly pinnately branched stems. The older parts of the plants are often tinged jet black. Rhizoids are difficult to find and are restricted to those parts of the branches and stems in contact with the substrate; they originate from circular clusters of initials abaxial to the leaf insertions. The genus has narrow, lanceolate-triangular, long-acuminate leaves that are twisted at the apex, strongly auriculate, with a U-shaped attachment to the stem. The leaf cells are long, porose, and densely pluripapillose, with the papillae arranged in seriate rows over the cell lumina. The extreme basal cells, however, are smooth and yellowish in color, and the alar cells are weakly differentiated. *Toloxis* is a dioicous genus and capsules are unknown in Central America. The Asian *T. semitorta* (Müll. Hal.) W. R. Buck has short, scabrous setae, oval capsules, smooth cucullate calyptrae, and reduced peristomes that consist of yellowish, linear, papillose exostome teeth and an endostome with a high basal membrane, no cilia, and rudimentary segments.

Toloxis is a segregate from the genus *Papillaria.* As noted by Buck (1998), it appears more similar to *Trachypodopsis* than to other *Papillaria* species. *Trachypodopsis* and *Toloxis* have similarly shaped, auriculate leaves, a U-shaped leaf attachment, and serrate leaf margins. *Trachypodopsis* differs from *Toloxis* in having bordered leaves; shorter leaf cells that have only 1–2 papillae over the cell lumina; longer setae (10–20 mm); exostome teeth that are weakly striate at base; and densely hairy calyptrae.

The name *Toloxis* is an anagram for *Loxotis*, which combines the Greek *loxox* (slanting or oblique) with *otos* (ear) and refers to its obliquely inserted, auriculate leaves.

Toloxis imponderosa (Taylor) W. R. Buck, Bryologist 97: 436. 1994. *Leskea imponderosa* Taylor, London J. Bot. 5: 62. 1846. *Pilotrichum imponderosum* (Taylor) Müll. Hal., Syn. Musc. Frond. 2: 174. 1851. *Meteorium imponderosum* (Taylor) Mitt., J. Linn. Soc., Bot. 12: 442. 1869. *Pilotrichella imponderosa* (Taylor) Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 225. 1872. *Papillaria imponderosa* (Taylor) Broth., Nat. Pflanzenfam. I(3): 815. 1906. *Loxotis imponderosa* (Taylor) W. R. Buck, J. Hattori Bot. Lab. 75: 59. 1994. Protologue. [Ecuador] Forest of Esmeraldos, *Prof. William Jameson*, (Dr. Greville's Herbarium).

Neckera oerstediana Müll. Hal., Syn. Musc. Frond. 2: 671. 1851. *Meteorium oerstedianum* (Müll. Hal.) Mitt., J. Linn. Soc., Bot. 12: 441. 1869. *Papillaria oerstediana* (Müll. Hal.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 266. 1877. Protologue. America centralis, Costa Rica in reg. montosa, elevatione 5000–8000′, ubi mens. Febr. et April. 1847. Sterilem legit *A. S. Oersted.*

Plants slender to medium-sized, green, yellow green, or yellow brown, often blackish with age, in mats or pendent masses. Stems pendent or creeping, to 15 cm long, irregularly or regularly pinnately branched; stems in cross section with sclerodermis of 3–5 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow, thick-walled, central strand small, weakly developed; paraphyllia absent; pseudoparaphyllia foliose; rhizoids sparse and present only where stems and branches contact the substrate, brown, smooth, not branched, from circular clusters of initials abaxial to the leaf insertions. Stem and branch leaves differing only in size, erect, somewhat incurved when dry, erect-spreading when wet, inserted in a U-shaped line, slenderly lanceolate-triangular, weakly plicate, 1–2 mm long, erect-clasping at base, gradually acuminate, apices twisted when wet or dry, auriculate, auricles undulate, not decurrent; margins plane, serrate throughout, at times dentate on the auricles; costae single, ending at or just above midleaf, in cross section cells homogeneous; upper and median cells densely seriate, pluripapillose, with 4–7 papillae over cell lumina, elongate to fusiform, thick-walled, porose, 40–60 × 4–5 μm, extreme basal cells elongate, porose, smooth; alar

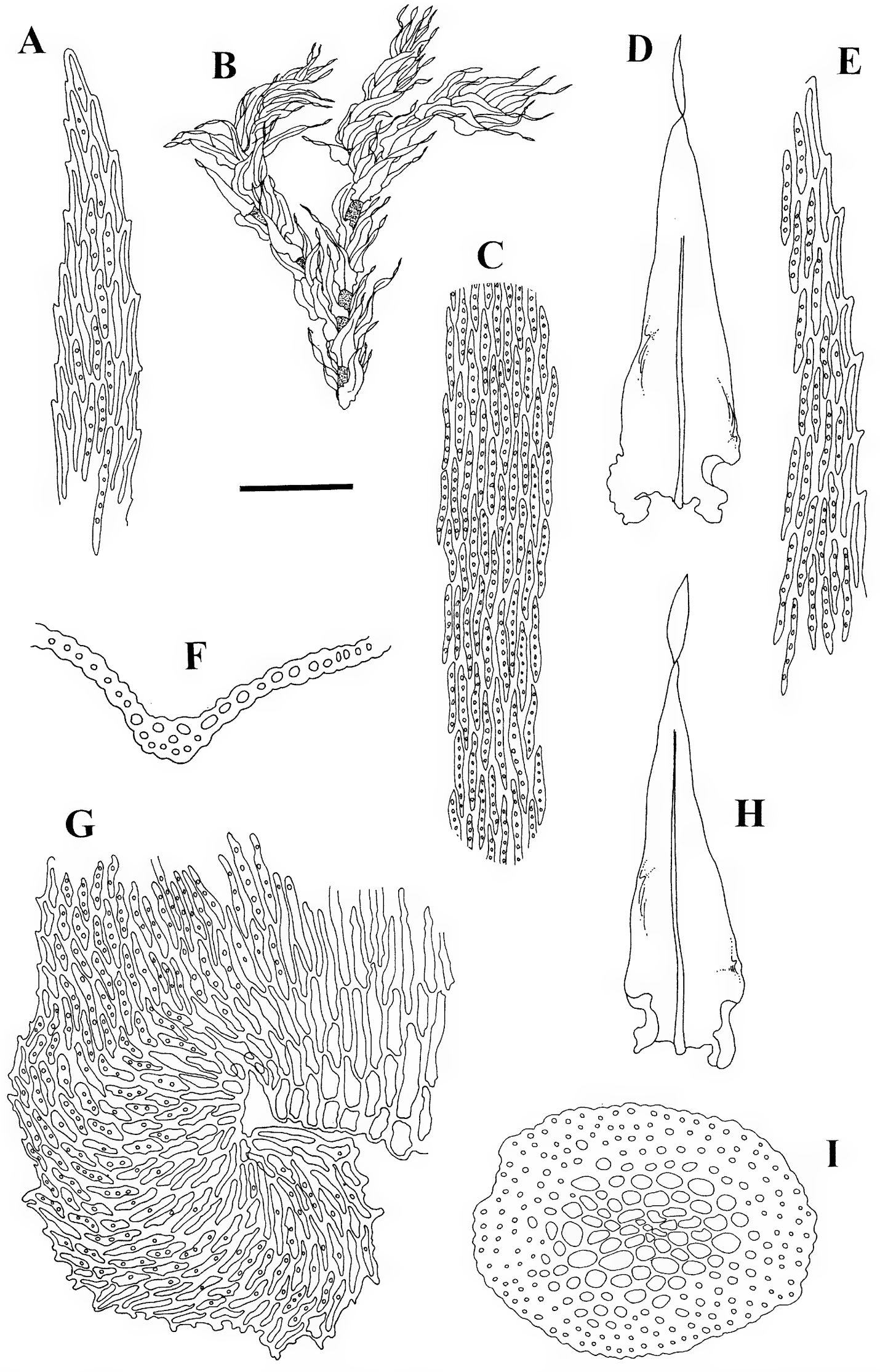
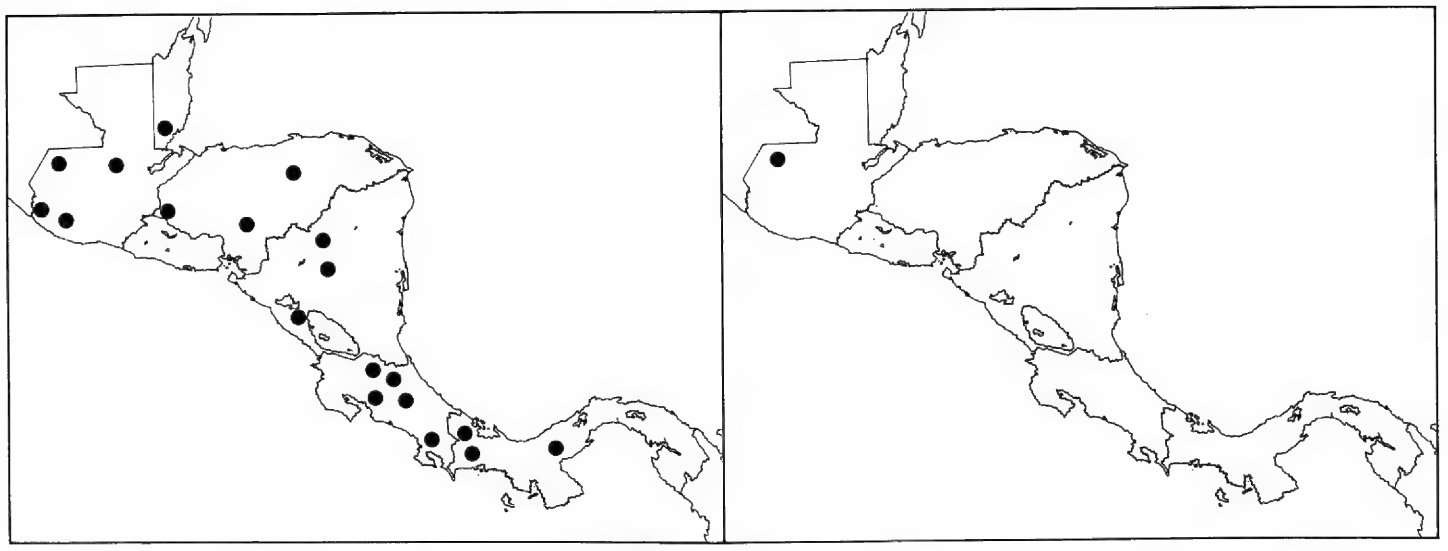


Figure 49. *Toloxis imponderosa*. A. Leaf apex. B. Habit. C. Median leaf cells. D & H. Leaves. E. Median leaf cells and margin. F. Costa in cross section. G. Alar cells. I. Stem in cross section. Scale in mm: bar = 0.04 (F); bar = 0.05 (A, C, E, G); bar = 0.06 (I); bar = 0.4 (D, H); bar = 2.0 (B). All figure parts from *Allen 12360*.



Toloxis imponderosa *Trachypodopsis serrulata* var. *crispatula*

cells irregularly quadrate or subrectangular, lightly papillose, thick-walled, porose, restricted to a few cells at the basal angles. Dioicous. Sporophytes unknown from Central America.

Illustrations. Bartram (1949, Fig. 119 A–B); Spessard (1980, Fig. 8); Sharp *et al.* (1994, Fig. 545 a–e); Churchill and Linares (1995, Fig. 124 h–j); Duarte Bello (1997, Pl. 199); Buck (1998, Pl. 105 1–6). Figure 49.

Habitat. On trees, pendent from branches, vines, and twigs, on stems and crowns of shrubs, in birds' nests, rotting logs, on ground at base of grass hummocks in cattle pastures, road banks, on boulders or rocks, often collected near or along streams; 900–2900 m.

Distribution in Central America. BELIZE. Toledo: *Gentle 6528* (MO). GUATEMALA. Alta Verapaz: *Standley 91474* (F, FH); Huehuetenango: *Steyermark 52009* (F, FH, US); San Marcos: *Standley 68474* (F, FH); Suchitepéquez: *Holdridge* (US). HONDURAS. Francisco Morazán: *Allen 12360* (MO); Ocotepeque: *Allen 14418* (FH, MO); Olancho: *Allen 12793C* (MO). NICARAGUA. Granada: *Miller et al. 1423* (MO); Jinotega: *Crosby 2777* (MO); Matagalpa: *Guzmán & Castro 2006* (HNMN, MO, NY, US). COSTA RICA. Alajuela: *Lyon 272* (CR, MO, NY); Cartago: *Standley 33682* (FH, US); Heredia: *Griffin et al. D261* (F, MO, US); Puntarenas: *Lyon 272* (CR, MO, NY); San José: *Croat 43388* (CR, MO). PANAMA. Bocas del Toro: *Allen 5261* (MO); Chiriquí: *Cornman 3181* (F, FH, MO, US); Coclé: *Crosby 4389* (MO).

World range: Mexico; Central America; Caribbean; Western and Northern South America, Brazil.

Toloxis imponderosa is a slender to medium-sized species usually found in pendent masses on tree trunks, branches, and twigs at medium to high elevations. It also grows occasionally on road and trail banks, boulders, or rotten logs. These terrestrial habits may be secondary, an indication that the species can continue to grow after falling to the ground. *Toloxis imponderosa* can be recognized in the field by its soft, slender appearance and its narrowly triangular-lanceolate leaves that are erect-incurved when dry, with consistently twisted apices. In Central America only *Trachypus bicolor* var. *viridulus* has a similar aspect in the field. That species, however, has somewhat larger, stiffer leaves than those of *Toloxis imponderosa*, and its leaf apices are not or only occasionally twisted. Distinctive microscopic features of *T. imponderosa* include its remarkably well-developed leaf auricles and seriate papillae arranged over the cell lumina.

In leaf shape *Toloxis imponderosa* is similar to *Trachypus bicolor* var. *viridulus* and *Trachypodopsis serrulata* var. *crispatula*. *Trachypus bicolor* var. *viridulus* and *Toloxis imponderosa* also have pluripapillose leaf cells, but in *Trachypus bicolor* var. *viridulus* the decurrent leaves have straight leaf insertions, and leaf cell papillae are arranged only over the cell walls. *Toloxis imponderosa* and *Trachypodopsis serrulata* var. *crispatula* both have auriculate leaves with U-shaped leaf insertions. *Trachypodopsis serrulata* var. *crispatula*, however, has 1–2 papillae scattered over the cell lumina and leaf auricles not nearly as well developed as those of *Toloxis imponderosa*.

9. *Trachypodopsis* M. Fleisch., Hedwigia 45: 64. 1905.

Plants medium-sized to robust, in green, yellow green, or yellow brown, dense or lax mats. Primary stems creeping, at times stoloniferous, stolons with reduced leaves; rhizoids dark brown, becoming blackish, smooth, not branched, from circular clusters of initials abaxial to the leaf insertions. Secondary stems erect, irregularly pinnately branched, not stipitate; cross section with sclerodermis, thick-walled cortical cells, and small central strand; paraphyllia absent; pseudoparaphyllia foliose. Secondary stem and branch leaves differing primarily in size, elongate-triangular to ovate-lanceolate, inserted in a U-shaped line, usually plicate, at times smooth, undulate to crispate above, long-acuminate, auriculate at base, shortly decurrent; margins plane, sharply serrate throughout; costae single, ending near the apex, in cross section with guide cells and single layer of dorsal and ventral stereid cells; upper and median cells smooth or with 1–2 papillae over the lumina, isodiametric to linear, thick-walled, usually porose, upper marginal cells elongate, smooth in 2–3 rows, often forming a more or less distinct border; extreme basal cells elongate-rectangular, porose, smooth; alar cells irregularly quadrate to rectangular, smooth, thick-walled, porose. Dioicous. Vaginulae densely hairy. Setae 10–20 mm long, somewhat flexuose, densely papillose. Capsules erect, subglobular to ovoid; exothecial cells at mouth small, round, thick-walled, in 3–6 rows, lower cells rounded to oblong, thick-walled; stomata phaneroporic, on capsule neck; opercula obliquely long-rostrate; annuli rudimentary, adhering to the mouth after dehiscence; peristome diplolepideous, yellowish white; exostome teeth linear, horizontally striate at base, papillose above; endostome with high, lightly papillose basal membranes, linear papillose, broadly perforate segments nearly as long as the exostome teeth, cilia absent. Calyptrae cucullate, densely hairy.

Trachypodopsis, a genus of five species (Zanten 1959), is found in Southeast Asia, Africa, the Hawaiian Islands, Central America, and Mexico. The genus mostly grows on trees, but occasionally is found on rocks or terrestrially. *Trachypodopsis* has medium-sized to robust plants with indistinctly creeping stems that give rise to simple or pinnately branched secondary stems. Plants of *Trachypodopsis* are greenish to yellow or reddish, but never tinged black. Rhizoids are more or less restricted to the creeping stems; they originate from circular clusters of initials abaxial to the leaf insertions, and are commonly black. The genus has ovate-lanceolate, long-acuminate, usually plicate and crispate leaves that are weakly to very strongly auriculate and have a long, single costa. Significantly, the leaves have a U-shaped leaf insertion, *i.e.*, the alar regions are attached very much higher on stems than the costa. The leaf cells are often porose and usually have 1–2 papillae over the cell lumina. One species (*T. auriculata* (Mitt.) M. Fleisch.) has smooth leaf cells. The alar cells are weakly to strongly differentiated. *Trachypodopsis* is a dioicous genus and capsules are rarely encountered. It has strongly papillose setae; erect capsules; hairy, cucullate calyptrae; a reduced peristome that consists of whitish yellow, linear exostome teeth that are horizontally striate at base but densely papillose above; and an endostome with a high basal membrane, long, linear segments, and no cilia. The single Central American collection belongs to the most widespread and variable species in the genus, *T. serrulata*.

Trachypodopsis is often placed in the Trachypodaceae, but Zanten (1959) indicated the genus closely resembled the Meteoriaceae in habit, leaf shape (especially in the consistent presence of leaf auricles), and sporophytic features. Buck (1994a) treated it in the Meteoriaceae. Within the Meteoriaceae (*sensu* Buck 1994a) *Trachypodopsis* is closest to *Duthiella* Müll. Hal. *ex* Broth. and *Aerobryopsis* M. Fleisch. These three genera all have U-shaped leaf insertions and are similar in leaf shape, cellular areolation and ornamentation, setae length, capsule shape, and overall peristome form. The *Duthiella* peristome is better developed than that of the other genera, and it has well-formed cilia in groups of three. All three genera have cucullate calyptrae, but only *Trachypodopsis* has a hairy calyptra. The genus was revised by Zanten (1959).

The name *Trachypodopsis* combines the Greek *trachys* (rough, shaggy) with *podos* (foot) and *opsis* (aspect, appearance). It refers to the similarity of *Trachypodopsis* and *Trachypus*.

Trachypodopsis serrulata (P. Beauv.) M. Fleisch. var. ***crispatula*** (Hook.) Zanten, Blumea 9: 521. 1959. *Hypnum crispatulum* Hook., Trans. Linn. Soc. London 9: 321. 1808. *Neckera crispatula* (Hook.) Hook., Musci. Exot. 2(19): 152. 1819. *Trachypus crispatulus* (Hook.) Mitt., J. Proc. Linn. Soc., Bot. Suppl. 1: 129. 1859. *Papillaria crispatula* (Hook.) A. Jaeger, Ber. Thätigk.

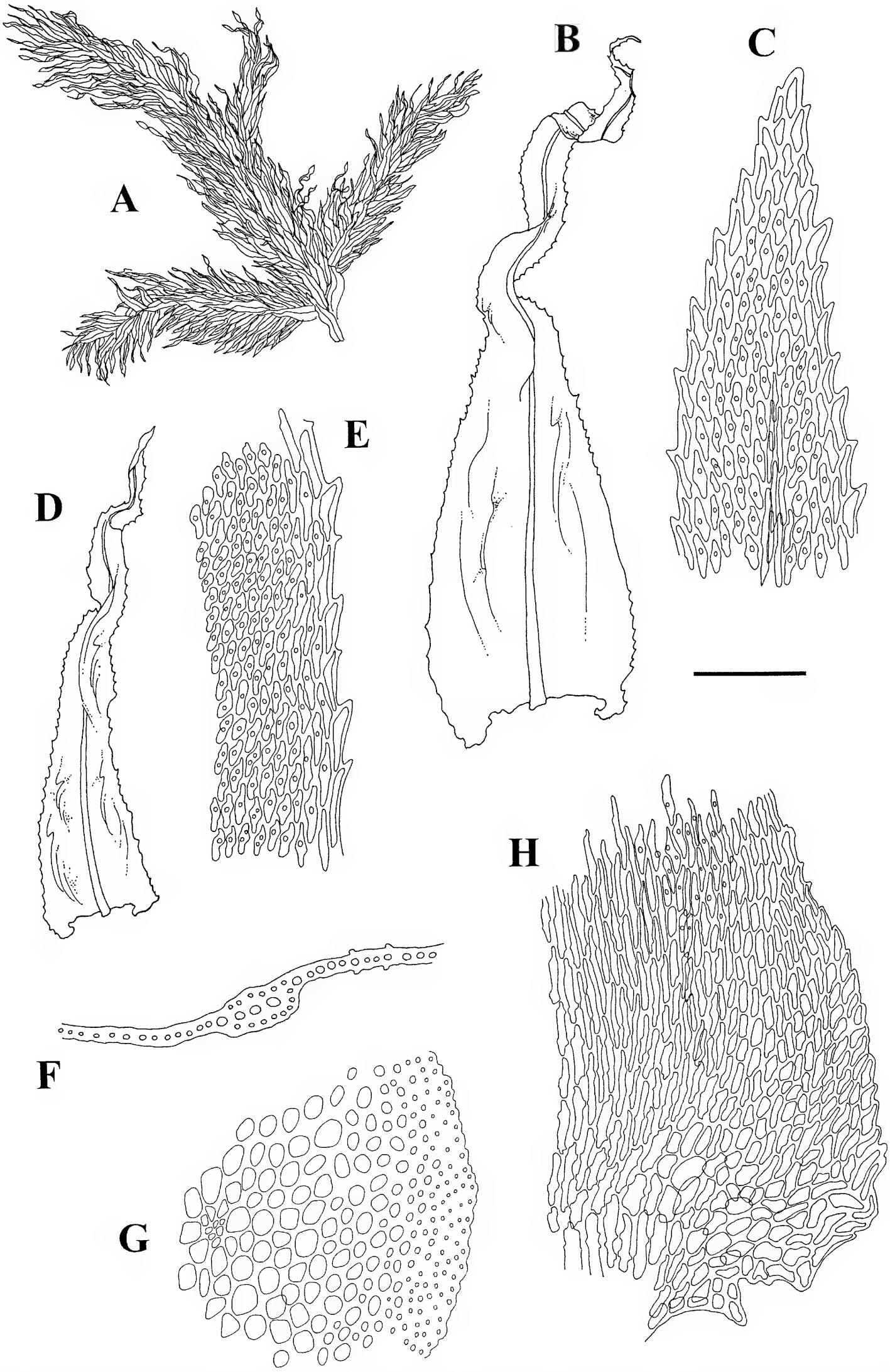


Figure 50. *Trachypodopsis serrulata* var. *crispatula*. A. Habit. B. Stem leaf. C. Leaf apex. D. Branch leaf. E. Median leaf cells and margin. F. Costa in cross section. G. Stem in cross section. H. Basal and alar cells. Scale in mm: bar = 0.05 (F); bar = 0.06 (C, E, H); bar = 0.08 (G); bar = 0.56 (B, D); bar = 4.0 (A). All figure parts from *Sharp 4901*.

St. Gallischen Naturwiss. Ges. 1875–76: 274. 1877. *Trachypodopsis crispatula* (Hook.) M. Fleisch., Hedwigia 45: 65. 1906. Protologue. Nepal, [*Francis Buchanan*]. Type (see Zanten 1959). Nepal, leg. *Buchanan* (BM, holotype).

Prionodon otiophylla Cardot, Rev. Bryol. 37: 7. 1910. *Trachypodopsis otiophylla* (Cardot) Cardot, Rev. Bryol. 38: 39. 1911. Protologue. [Mexico] État de Morelos: près de Cuernavaca, 1908 (*Pringle, n. 15184*). Type. Plantae Mexicanae. State of Morelos. Near Cuernavaca. On rock knobs, Parque, 7500 ft., 27 July 1908, *C. G. Pringle 15184* (FH, NY, isotypes).

Plants medium-sized, in green, yellow green, or yellow brown, dense or lax mats. Primary stems creeping, at times stoloniferous, stolons with reduced leaves; rhizoids dark brown, becoming blackish, smooth, not branched, from circular clusters of initials abaxial to the leaf insertions. Secondary stems erect, irregularly pinnately branched, not stipitate, 4–10 cm long; stems in cross section with sclerodermis of 3–5 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, thick-walled, central strand small; paraphyllia absent; pseudoparaphyllia foliose. Secondary stem and branch leaves differing in size and auricle development, erect to spreading, crispate above when dry, wide-spreading when wet, elongate-triangular to ovate-lanceolate, to 4 mm long, plicate, undulate to crispate above, erect at base, long-acuminate, distinctly auriculate at base, shortly decurrent; margins plane, sharply serrate throughout; costae single, ending near the apex, in cross section with guide cells and single layer of dorsal and ventral stereid cells; upper and median cells with 1–2 papillae over the lumina, fusiform to elongate, thick-walled, usually porose, 18–40 × 4 µm, upper marginal cells longer, smooth, in 2–3 rows, forming a more or less distinct border; extreme basal cells elongate-rectangular, porose, smooth, 24–50 × 2–4 µm; alar cells weakly developed, irregularly quadrate to rectangular, smooth, thick-walled, porose. Dioicous. Sporophytes unknown from Central America.

Illustrations. Hooker (1808, Pl. 28 4); Bartram (1939, Pl. 14 243); Bartram (1949, Fig. 112 D–F); Zanten (1959, Pl. 4 1c & 1d); Gangulee (1976, Fig. 597); Sharp *et al.* (1994, Fig. 522 d–f). Figure 50.

Habitat. On logs; 2438 m.

Distribution in Central America. GUATEMALA. Huehuetenango: *Sharp 4901* (F, FH).

World range: Mexico; Central America; China; Indian Subcontinent, Indo-China, Malesia.

Trachypodopsis serrulata var. *crispatula* is a medium-sized species known in Central America from a single Guatemalan collection. It has matted, irregularly pinnately branched stems and elongate triangular to narrowly ovate-lanceolate leaves. The leaves are auriculate; however, the auricles on the stems leaves are much better developed than those on the branch leaves. Other distinctive leaf features of *T. serrulata* var. *crispatula* include its sharply serrate leaf margins, weakly developed alar cells, and 1–2 papillae scattered over the cell lumina.

Trachypodopsis serrulata var. *crispatula* is similar in aspect to *Toloxis imponderosa* and *Trachypus bicolor* var. *viridulus*, and they all have similarly shaped leaves. *Toloxis imponderosa* and *Trachypodopsis serrulata* var. *crispatula* are also similar in having auriculate leaves with U-shaped leaf insertions. *Toloxis imponderosa* and *Trachypus bicolor* var. *viridulus* differ from it in having pluripapillose leaf cells with the papillae seriately arranged either over the cell lumina or the cell walls. In *Toloxis imponderosa* the leaf auricles are remarkably well developed, and its leaf apices, whether wet or dry, are consistently twisted.

This species has long been known in Central America as *T. otiophylla.* Cardot (1911), however, considered *T. otiophylla* very close to *T. crispatula*, and Bartram (1949) found little or no vegetative differences between the two taxa. Zanten (1959), in a revision of *Trachypodopsis*, regarded *T. serrulata* an extremely variable species with three varieties (var. *serrulata*, var. *crispatula*, and var. *guilbertii*), but noted there were many collections intermediate in form between the varieties. Zanten found that all the features of *T. otiophylla* fell "entirely within the limits of *T. serrulata* var. *crispatula*." Crum (1994d), while noting the gametophytic similarity between *T. otiophylla*, *T. serrulata*, and *T. crispatula*, continued to recognize *T. otiophylla* because its sporophytes are unknown.

10. *Trachypus* Reinw. & Hornsch., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 14(2): 708. 1828. *Papillaria* sect. *Trachypus* (Reinw. & Hornsch.) A. Jaeger, Ber. Thätigk. St. Gallischen

Naturwiss. Ges. 1875–76: 273. 1877. *Meteorium* sect. *Trachypus* (Reinw. & Hornsch.) Mitt., Trans. Linn. Soc. London, Bot. II, 3: 173. 1891.

Plants slender to robust, green, yellow green, or yellow brown, often blackish with age, in dense or lax mats. Primary stems creeping, at times stoloniferous, stolons with reduced, scale-like leaves; rhizoids brown when young, becoming jet black, smooth, not branched, from circular clusters of initials abaxial to the leaf insertions. Secondary stems erect, simple or irregularly to regularly pinnately branched, not stipitate; in cross section with sclerodermis, enlarged, firm-walled cortex, central strand present or absent; paraphyllia absent; pseudoparaphyllia foliose. Stem and branch leaves isophyllous or heterophyllous, appressed to horizontally spreading when dry, erect-spreading to spreading when wet, inserted in a straight line, variously clasping at base, plicate or plane, acuminate, often ending in short, hyaline hair-points, not or weakly auriculate, shortly decurrent; margins plane throughout or narrowly recurved below, serrulate below, papillose-crenulate above; costae single, ending above midleaf, in cross section cells homogeneous; upper and median cells densely seriately pluripapillose, papillae over cell walls, long-hexagonal to linear, thick-walled, porose; extreme basal cells elongate, porose, smooth; alar cells weakly developed, quadrate to rectangular, lightly papillose, thick-walled, porose. Dioicous. Setae long, erect or flexuose, scabrose-papillose, red brown. Capsules globose to ovoid; exothecial cells hexagonal to rectangular, firm-walled; stomata on capsule neck; opercula obliquely long-rostrate; annuli rudimentary, of small, firm-walled cells; peristome diplolepideous; exostome teeth yellowish, linear, papillose; endostome papillose, basal membranes high, segments rudimentary, cilia absent. Calyptrae cucullate, split on one side nearly the entire length, densely hairy.

Trachypus is a genus of five species (Zanten 1959) found in the tropical regions of the world, with its center of distribution in Southeast Asia. The genus grows on trees, rocks, or terrestrially, but in Central America it appears to be more commonly corticolous. Central American plants of *Trachypus* are medium-sized, and they have indistinctly creeping stems that give rise to simple or pinnately branched secondary stems. The plants are frequently tinged jet black. Rhizoids are common on the creeping stems, but horizontal secondary stems also have rhizoids. They originate from circular clusters of initials abaxial to the leaf insertions, and are commonly black. The genus has ovate-lanceolate, long-acuminate leaves that are variously auriculate and have long, single costae. The leaf cells are mostly long, usually porose, and densely pluripapillose, with the papillae arranged in seriate rows over the cell walls. The extreme basal cells, however, are smooth and yellowish in color, and the alar cells are weakly differentiated. *Trachypus* is a dioicous genus and capsules are rarely encountered. It has long, scabrous setae, erect capsules, densely hairy calyptrae, a rudimentary annulus, and a reduced peristome that consists of whitish yellow, linear, papillose exostome teeth and an endostome with a high basal membrane, no cilia, and rudimentary segments.

The calyptrae of *Trachypus* were originally described as "conico-campanulata" (Reinwardt & Hornschuch 1829), and Fleischer (1908) called them "kegelmützenförmig." Zanten (1959), however, attributed mitriform or cucullate calyptrae to the genus, and Buck (1994a, 1998) described only cucullate calyptrae for the genus. The calyptrae fall early in *Trachypus*; they are long-cylindrical in shape and, as noted by Bartram (1939), split nearly the entire length along one side. The odd form of the *Trachypus* calyptra and its early fall from the capsules appear to be correlated with the development of its strongly oblique, long-rostrate opercula.

Trachypus is often placed in the Trachypodaceae; Buck (1994a, 1998) treated it in the Meteoriaceae. Although the long, scabrous setae in *Trachypus* seem at odds in the Meteoriaceae, the genus resembles members of that family in plant aspect and peristome form. Furthermore, *Cryptopapillaria* and *Trachypus* have a similar type of leaf cell ornamentation, and the presence of an intensely black coloration in its gametophytes is an important indication of the Meteoriaceae (see Allen & Magill 2003). The genus was revised by Zanten (1959).

The name *Trachypus* combines the Greek *trachys* (rough, shaggy) with *-pus* (footed) and perhaps refers to its scabrose papillose setae.

Trachypus bicolor Reinw. & Hornsch. var. ***viridulus*** (Mitt.) Zanten, Blumea 9: 499. 1959. *Neckera viridula* Mitt., Hooker's J. Bot. Kew Gard. Misc. 3: 351. 1851. *Meteorium viridulum* (Mitt.) Mitt., J. Linn. Soc., Bot. 12: 443. 1869. *Papillaria viridula* (Mitt.) A. Jaeger, Ber. Thätigk. St. Galli-

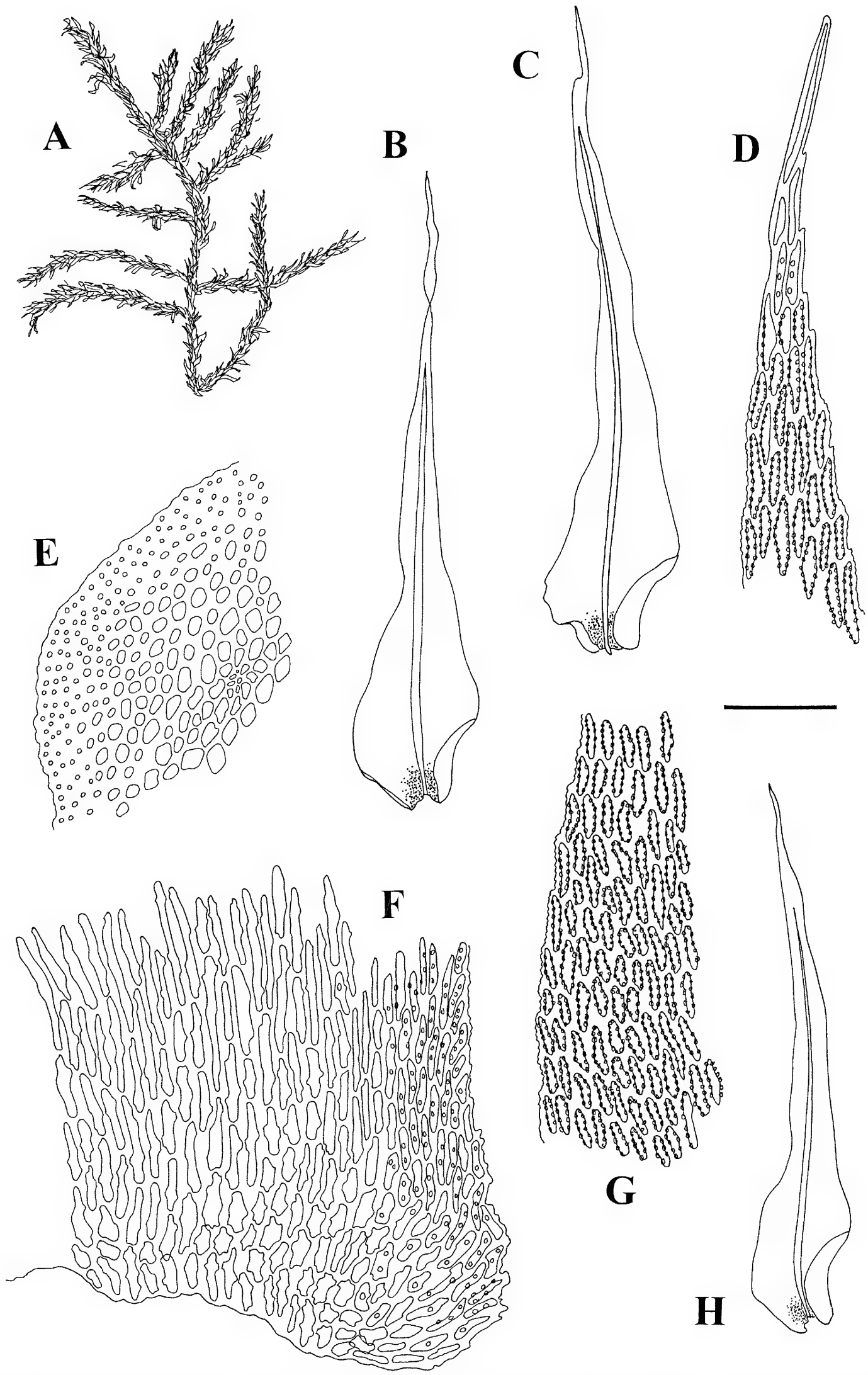
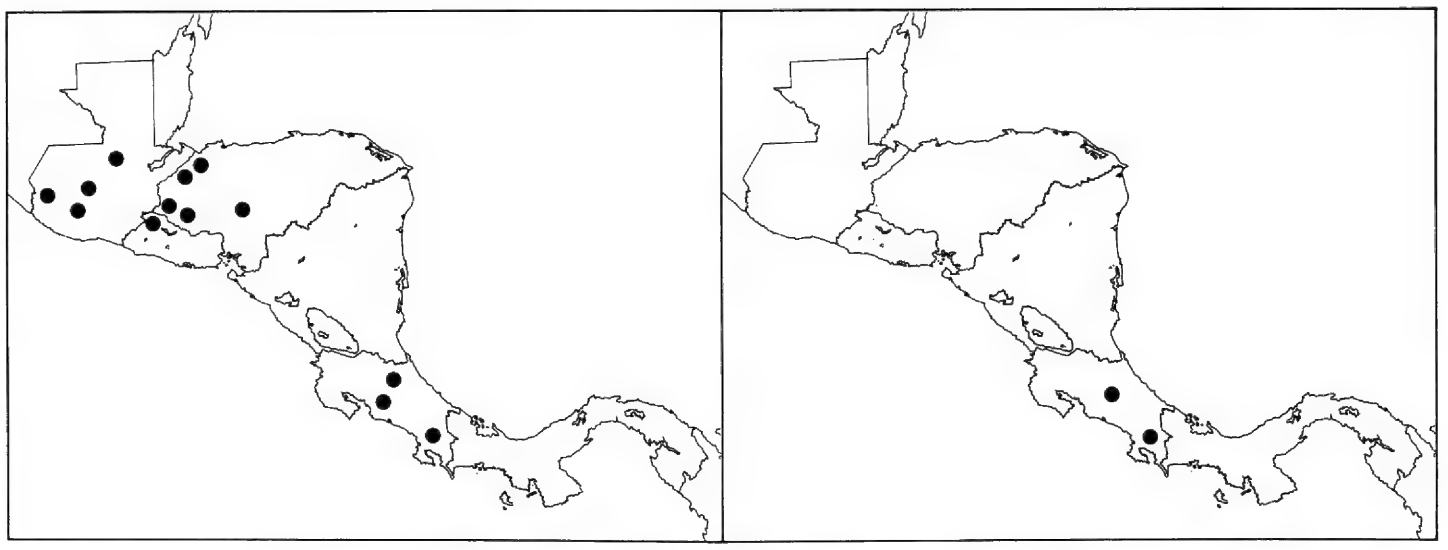


Figure 51. *Trachypus bicolor* var. *viridulus*. A. Habit. B, C & H. Leaves. D. Leaf apex. E. Stem in cross section. F. Basal and alar cells. G. Median leaf cells. Scale in mm: bar = 0.05 (D, F, G); bar = 0.06 (E); bar = 0.4 (B, C, H); bar = 6.4 (A). F & G from *Crosby 3598*; all other figure parts from *Allen 14242*.



Trachypus bicolor var. *viridulus* *Zelometeorium allionii*

schen Naturwiss. Ges. 1875–76: 267. 1877. *Trachypus viridulus* (Mitt.) Broth., Nat. Pflanzenfam. I(3): 830. 1906. Protologue. [Ecuador, Vicinity of Quito, *Professor W. Jameson*] *No. 58.*

Pilotrichella longifolia Schimp. *ex* Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 225. 1872. *Papillaria longifolia* (Besch.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 265. 1877. Protologue. [Mexico] Orizaba (*F. Müller* in herb. Schimper).

Plants medium-sized, green, yellow green, or yellow brown, often blackish with age, in dense or lax mats. Primary stems creeping, at times stoloniferous, stolons with reduced, scale-like leaves; rhizoids brown when young, becoming jet black, smooth, not branched, from circular clusters of initials abaxial to the leaf insertions. Secondary stems erect, simple or irregularly to regularly pinnately branched, not stipitate, 1–15 cm long; stems in cross section with sclerodermis of 3–5 rows of small, red brown, thick-walled cells, cortical cells enlarged, yellow to hyaline, firm-walled, central strand small, weakly developed; paraphyllia absent; pseudoparaphyllia foliose. Secondary stem and branch leaves differing only in size. Leaves erect to spreading, somewhat crispate above when dry, erect-spreading when wet, ovate-lanceolate, inserted in a straight line, 2–3 mm long, plane to somewhat plicate, erect-clasping at base, acuminate, ending in short hyaline hair-points, weakly auriculate, shortly decurrent; margins plane or narrowly recurved below, serrulate below, papillose-crenulate above; costae single, ending above midleaf, in cross section cells homogeneous; upper and median cells densely seriately pluripapillose, over cell walls, long-hexagonal to linear, thick-walled, porose, 30–40 × 4–5 µm; extreme basal cells elongate, porose, smooth; alar cells weakly developed, quadrate to rectangular, lightly papillose, thick-walled, porose. Dioicous. Sporophytes unknown from Central America.

Illustrations. Bartram (1949, Fig. 112 A–C); Sharp *et al.* (1994, Fig. 522 a–c); Churchill and Linares (1995, Fig. 193); Duarte Bello (1997, Pl. 181); Buck (1998, Pl. 106); Magill and Rooy (1998, Fig. 156 9–16). Figure 51.

Habitat. On tree (*Cupressus*, *Pinus*) trunks, vines, logs, fallen branches, and terrestrial on road banks, occasionally on rocks; 1278–2896 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: *Standley 71091* (FH); Chimaltenango: *Standley 58781* (F, FH, US); San Marcos: *Sharp 5487* (F, FH, NY); Sololá: *Standley 62361* (F, FH). EL SALVADOR. Santa Ana: *Davidse et al. 37194* (MO). HONDURAS. Cortés: *Allen 14242* (MO); Francisco Morazán: *Allen 12395* (MO); Lempira: *Allen 12093* (MO); Ocotepeque: *Allen 14475* (MO); Santa Bárbara: *Allen 11629* (MO). COSTA RICA. Heredia: *Crosby 9911* (CR, MO); Puntarenas: *Crosby 3598* (MO); San José: *Bowers 244b* (MO).

World range: Mexico; Central America; Caribbean; Western South America; West Central Tropical Africa, Southern Africa, Western Indian Ocean; Eastern Asia; Indian Subcontinent, Indo-China, Malesia.

Trachypus bicolor var. *viridulus* is a medium to high elevation species found in Central America on a variety of substrates, but more commonly occurring on tree trunks. It often has matted, pinnately branched stems and narrowly ovate-lanceolate leaves. The leaves are weakly auriculate, with single costae and weakly developed alar cells. The distinctions between the stolons, stems, and branches in *T. bicolor* var. *viridulus* are often weak, with intermediate forms common, and each having the ability to change from one form to another. *Trachypus bicolor* var. *viridulus* has the color, aspect, and leaf shape of *Toloxis imponderosa* or *Trachypodopsis serrulata* var. *crispatula*. *Trachypodopsis serrulata* var. *crispatula* differs from it in having leaf cells with 1–2 papillae scattered over the lumina, and U-shaped leaf insertions. *Toloxis imponderosa* has U-shaped leaf insertions, densely pluripapillose leaf cells with the papillae seriately arranged over the cell lumina, remarkably well-developed leaf auricles, and leaf apices that are consistently twisted. *Cryptopapillaria penicillata* has a somewhat similar type of leaf cell areolation, with multiple papillae arranged over the cell walls, but also found scattered over the lumina. It also differs from *Trachypus bicolor* var. *viridulus* in having ovate-triangular leaves that are smoothly imbricate rather than erect-spreading when dry and strongly auriculate leaves with short, oval cells.

Zanten (1959) was the first to associate this taxon with *T. bicolor* Reinw. & Hornsch. He also attributed a wide geographic distribution to *T. bicolor* var. *viridulus*. Despite the presence of numerous intermediate forms, the variety was recognized on the basis of its somewhat smaller size, flaccid, laxly foliate stems, and the lack of a blackish coloration. This last distinction is, however, not valid since Central American collections often have a blackish coloration. Zanten (1959) described the stems of *T. bicolor* as lacking a central strand, but Central American and West Indian (see Buck 1998) collections of *T. bicolor* var. *viridulus* have a weakly developed central strand. An examination of Asian material of *T. bicolor* shows the central strand to vary from absent to very weakly developed. Crum (1994d) and Buck (1998) recognized this taxon as a species (*Trachypus viridulus*) restricted to the Neotropics and differing from *T. bicolor* in its smaller size and phytogeographic distribution.

11. *Zelometeorium* Manuel, J. Hattori Bot. Lab. 43: 110. 1977.

Meteorium sect. *Squarridium* Müll. Hal., Linnaea 42: 492. 1879, invalid name, lacks a description.
Meteoriopsis sect. *Squarridium* Müll. Hal. *ex* Broth., Nat. Pflanzenfam. I(3): 825. 1906, illegitimate name, includes type of *Meteoriopsis*.

Plants slender to medium-sized, often in dense, creeping or pendent, epiphytic masses. Primary stems with small, thick-walled, epidermal cells, cortical cells enlarged, central strand small; irregularly branched, branches short to medium-sized; rhizoids in dense clusters, smooth, not branched, from circular clusters of initials abaxial to the leaf insertions. Leaves trimorphic: stolon/primary stem leaves, secondary stem leaves, and branch leaves. Stolon/primary stem leaves erect, strongly clasping, ovate-lanceolate, apices long-acuminate to piliferous, sometimes twisted; margins generally plane, subentire; costae single, slender, tapering to the apex, commonly ending above midleaf, at times ending in a small spine; median cells linear-flexuose, firm-walled, often porose; alar cells weakly differentiated. Secondary stem leaves erect-appressed, broadly ovate-lanceolate, otherwise similar to primary stem leaves. Branch leaves closely spaced, wide spreading, squarrose, or squarrose-recurved, erect, sheathing or more or less spreading at base, narrowly elliptic, ovate-lanceolate, ovate-acuminate, broadly ovate to orbicular, short- to long-acuminate or apiculate; margins plane or narrowly recurved below, subentire to serrulate; costae single, slender, tapering to the apex, ending 1/2–3/4 the leaf length; median cells fusiform to linear-flexuose, firm-walled, not porose; alar cells weakly differentiated or moderately differentiated in bulging excavate groups, cells subquadrate, firm- to thick-walled, at times porose. Asexual reproduction occasionally by branchlets from branch leaf axils. Dioicous. Perichaetia lateral on stems and branches. Setae short. Capsules exserted, erect, ellipsoid to cylindric, constricted at neck; exothecial cells quadrate to oblate at the mouth, irregularly rectangular below, with thick vertical walls and thin horizontal walls; stomata superficial on neck; opercula shortly rostrate; annuli rudimentary, of several rows of thick-walled cells; exostome teeth linear, papillose; endostome lightly papillose, 2/3 the exostome length, basal membranes low, segments linear, perforate below, cilia rudimentary or absent. Calyptrae mitrate, lobed, densely hairy.

Zelometeorium is a genus of five species (Manuel 1977a) widely distributed in the Neotropics. It extends as far north as northeast Mexico and the southern tip of Florida. As with the genus *Squamidium*, one species (*Z. ambiguum* (Hornsch. *in* Mart.) Manuel) occurs as a disjunct in central Africa. There are four species of *Zelometeorium* in Central America; the fifth species (*Z. patens*) occurs in Colombia and western Venezuela and may eventually be found in Panama. It is a fairly common genus in the forests of Central America. The plants are predominantly epiphytic and often grow pendent, but in wet, shaded places they can also be found terrestrially or on rocks and boulders. This latter habitat appears to be secondary, representing plants that have persisted after falling from trunks or branches. As with many other mosses that often grow pendent, *Zelometeorium* has trimorphic leaves associated with their stolons, secondary stems, and branches. Stolon and stem leaves in *Zelometeorium* are strongly clasping and generally piliferous, while the branch leaves are weakly clasping to more or less spreading from the insertions and more shortly pointed. Leaves at the tips of the stolons, stems, and branches have the ability to change from one to another form in apparent response to changes in orientation. The leaf cells in *Zelometeorium* are elongate throughout, smooth, often porose, and the alar cells are weakly differentiated. Its leaves have variously serrulate margins and weak, single costae that at times end in projecting spines. The sporophytes in this genus have shortly exserted, cylindrical capsules, with linear, papillose exostome teeth, and weakly developed endostomes that mostly lack cilia. The calyptrae in *Zelometeorium* are mitrate and densely hairy.

Zelometeorium and *Squamidium* have been considered closely related (Allen & Crosby 1986b) primarily on the basis of their sporophytes; indeed, the sporophytes of *Zelometeorium* and *Squamidium* sect. *Macrosquamidium* are essentially identical in all features. The gametophytes of *Squamidium* differ from those of *Zelometeorium* only in having erect to erect-spreading branch leaves, more strongly developed alar cells, and costae that do not end in a projecting spine. *Zelometeorium* was monographed by Manuel (1977a).

The name *Zelometeorium* combines the Greek *zelo* (emulate, envy, or rival) with the generic name *Meteorium*.

1. Branch leaves with sheathing part 0.3–0.6 the leaf length . . . . . 1. *Z. allionii*
1. Branch leaves with sheathing part less than 0.3 the leaf length 2
    2. Stem and branch leaves erect; leaf margins consistently recurved to revolute near base . . . . . 2. *Z. ambiguum*
    2. Stem leaves erect, branch leaves spreading to squarrose-recurved; margins of branch leaves plane or narrowly recurved at base 3

3. Branch leaves broadly ovate to orbicular; apices acute to short-acuminate, often apiculate . . . . . 4. *Z. recurvifolium*
3. Branch leaves ovate-lanceolate to ovate-acuminate; apices short- to long-acuminate, never apiculate . . . . . 3. *Z. patulum*

1. *Zelometeorium allionii* Manuel, J. Hattori Bot. Lab. 43: 113. 1977. Protologue. [Ecuador] Lecus n'am hes Cruces pondens ad arbores 900/1000, *Allioni*, Oct. 1910. Type (see Manuel 1977a). H, holotype.

Plants medium-sized, green to yellow green, in dense, creeping or pendent, epiphytic masses. Primary stems to 15 cm long, irregularly branched, branches generally short, to 1 cm long; stems in cross section with 3–5 rows of small, thick-walled, yellow to red epidermal cells, cortical cells enlarged, firm-walled, yellow to hyaline, central strand small; rhizoids in dense clusters, dark brown to blackish, smooth, not branched, from circular clusters of initials abaxial to the leaf insertions. Leaves trimorphic: stolon/primary stem leaves, secondary stem leaves, and branch leaves. Stolon/primary stem leaves erect, strongly clasping, ovate-lanceolate, 1.8–2.8 mm long; apices long-acuminate to piliferous, sometimes twisted; margins generally plane, subentire to serrulate; costae single, slender, tapering to the apex, commonly ending above midleaf, at times ending in a small spine; median cells linear-flexuose, 50–75 × 5–8 µm, firm-walled, often porose; alar cells moderately differentiated in bulging, excavate groups. Secondary stem leaves erect-appressed, broadly ovate-lanceolate, to 2.0 mm long, otherwise similar to primary stem leaves. Branch leaves closely spaced, squarrose to squarrose-

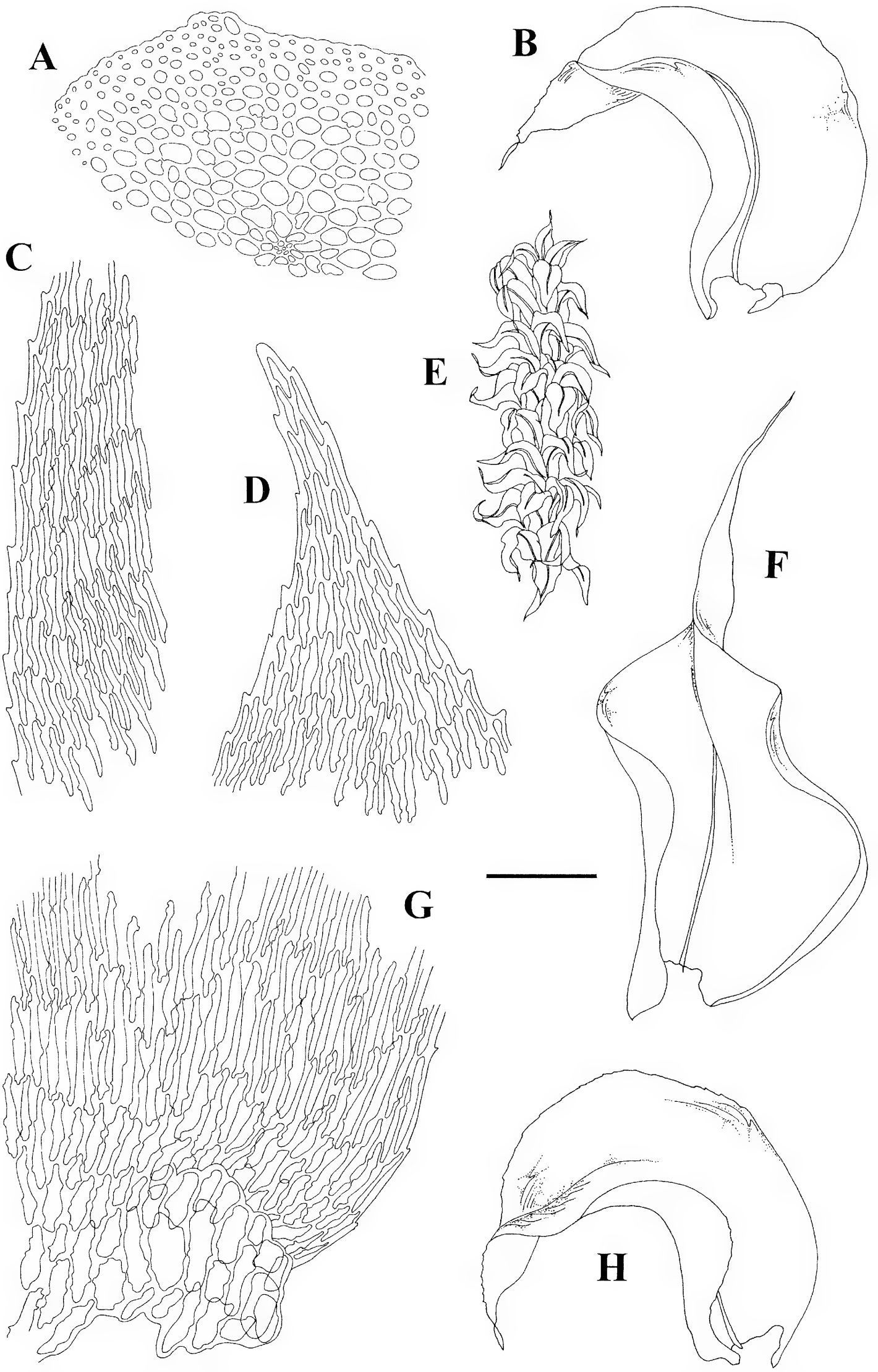


Figure 52. *Zelometeorium allionii*. A. Stem in cross section. B & H. Branch leaves. C. Median leaf cells and margin. D. Leaf apex. E. Habit. F. Stem leaf. G. Basal and alar cells. Scale in mm: bar = 0.06 (C, D, G); bar = 0.08 (A); bar = 0.5 (B, F, H); bar = 2.5 (E). All figure parts from *Gómez 25410.*

recurved, erect sheathing at base from 0.3–0.6 the leaf length, narrowly elliptic to ovate-lanceolate, 1.0–1.7 mm long; apices abruptly narrowed, short-acuminate; margins plane, serrulate to serrate throughout; costae single, slender, tapering to the apex, ending 1/2–3/4 the leaf length, not apparently ending in a small spine; cells porose throughout, median cells fusiform to linear-flexuose, 50–80 µm long, firm-walled; alar cells moderately differentiated in bulging excavate groups, cells subquadrate to subrectangular, firm- to thick-walled, porose. Dioicous. Sporophytes not seen, description from Manuel (1977a). Setae less than capsule length. Capsules erect, emergent, elliptic to ovate, 1.3–1.8 × 0.9–0.95 mm; exothecial cells quadrate to rectangular, thick-walled, with oblique end-walls; opercula 1.0–1.6 mm long, shortly rostrate; exostome teeth linear, 800–880 µm long, papillose; endostome papillose, basal membranes low, segments 720–760 µm long, cilia absent. Spores 22.5–27.5 µm. Calyptrae mitrate, pilose, 1.9–2.2 mm long.

Illustrations. Manuel (1977a, Fig. 5). Figure 52.

Habitat. Pendent from branches, on tree trunks, twigs, and rotting logs; 1140–1400 m.

Distribution in Central America. COSTA RICA. Cartago: *Crosby 2539* (MO); Puntarenas: *Gómez 25410* (CR, MO, NY).

World range: Central America; Western South America.

Zelometeorium allionii is a medium-sized species with squarrose to squarrose-recurved branch leaves. The leaf cells in *Z. allionii* are porose throughout, and the alar cells, which occur in bulging excavate groups, are exceptionally well developed for the genus. Squarrose to squarrose-recurved leaves are also a consistent feature of *Z. recurvifolium*, and occasionally *Z. patulum* has that type of leaf form. In those two species, however, the branch leaves are only shortly erect at base, with the sheathing part never more than 0.3 the leaf length. The presence of at least some more or less orbicular, apiculate branch leaves in *Z. recurvifolium* further distinguishes it from *Z. allionii*. Most collections of *Z. patulum* differ from *Z. allionii* in having only wide-spreading to weakly squarrose leaves. Collections of *Z. patulum* with squarrose-recurved leaves differ from *Z. allionii* in having more weakly developed alar cells, less porose laminal cells, and shortly sheathing leaf bases. *Zelometeorium patens* (Hook.) Manuel is present nearby in Colombia and western Venezuela. It is very similar to *Z. allionii* in overall aspect, but differs in having at least some ovate to widely ovate branch leaves with acute to obtuse, apiculate apices.

2. *Zelometeorium ambiguum* (Hornsch. *in* Mart.) Manuel, J. Hattori Bot. Lab. 43: 113. 1977. *Pilotrichum ambiguum* Hornsch. *in* Mart., Fl. Brasil. 1(2): 59. 1840. *Meteorium ambiguum* (Hornsch. *in* Mart.) Mitt., J. Linn. Soc., Bot. 12: 446. 1869. *Meteoriopsis ambiguum* (Hornsch. *in* Mart.) Broth., Nat. Pflanzenfam. I(3): 826. 1906. Protologue. In Brasilia australiori: *Sellow*. Types (see Manuel 1977a). BM, lectotype; BM, isotype.

Meteorium wagneri Lorentz, Moosstudien 165. 1864. Protologue. Chiriqui in Panama leg. *M. Wagner* April 1858. Types. Chiriqui in Panama leg. *M. Wagner* 1858 (BM, NY, isotypes).

Plants medium-sized, green to yellow green, in dense, creeping or pendent, epiphytic masses. Primary stems to 15 cm long; stems in cross section with 3–4 rows of small, thick-walled, yellow to red epidermal cells, cortical cells enlarged, firm-walled, yellow to hyaline, central strand small; irregularly branched, branches generally short, 0.5–2.0 cm long; rhizoids sparse, when present in small groups, reddish brown, smooth, not branched, from circular clusters of initials abaxial to the leaf insertions. Leaves dimorphic: stem leaves and branch leaves. Stem leaves erect, strongly clasping, ovate-lanceolate, 1.0–1.7 mm long; apices long-acuminate to piliferous; margins plane above, revolute below, subentire to serrulate; costae single, slender, tapering to the apex, commonly ending at or slightly above midleaf; median cells linear-flexuose, 35–60 × 5–8 µm, firm-walled, often porose; alar cells moderately differentiated in bulging, excavate groups. Branch leaves closely spaced, erect to somewhat spreading, weakly clasping at base, ovate to broadly ovate, 0.6–1.2 mm long, short-acuminate; margins plane, revolute below, serrulate to serrate throughout; costae single, slender, tapering to the apex, ending 1/2–3/4 the leaf length; median cells fusiform to linear-flexuose, 35–75 µm long, firm-walled; alar cells moderately differentiated in bulging excavate groups, cells subquadrate to subrec-

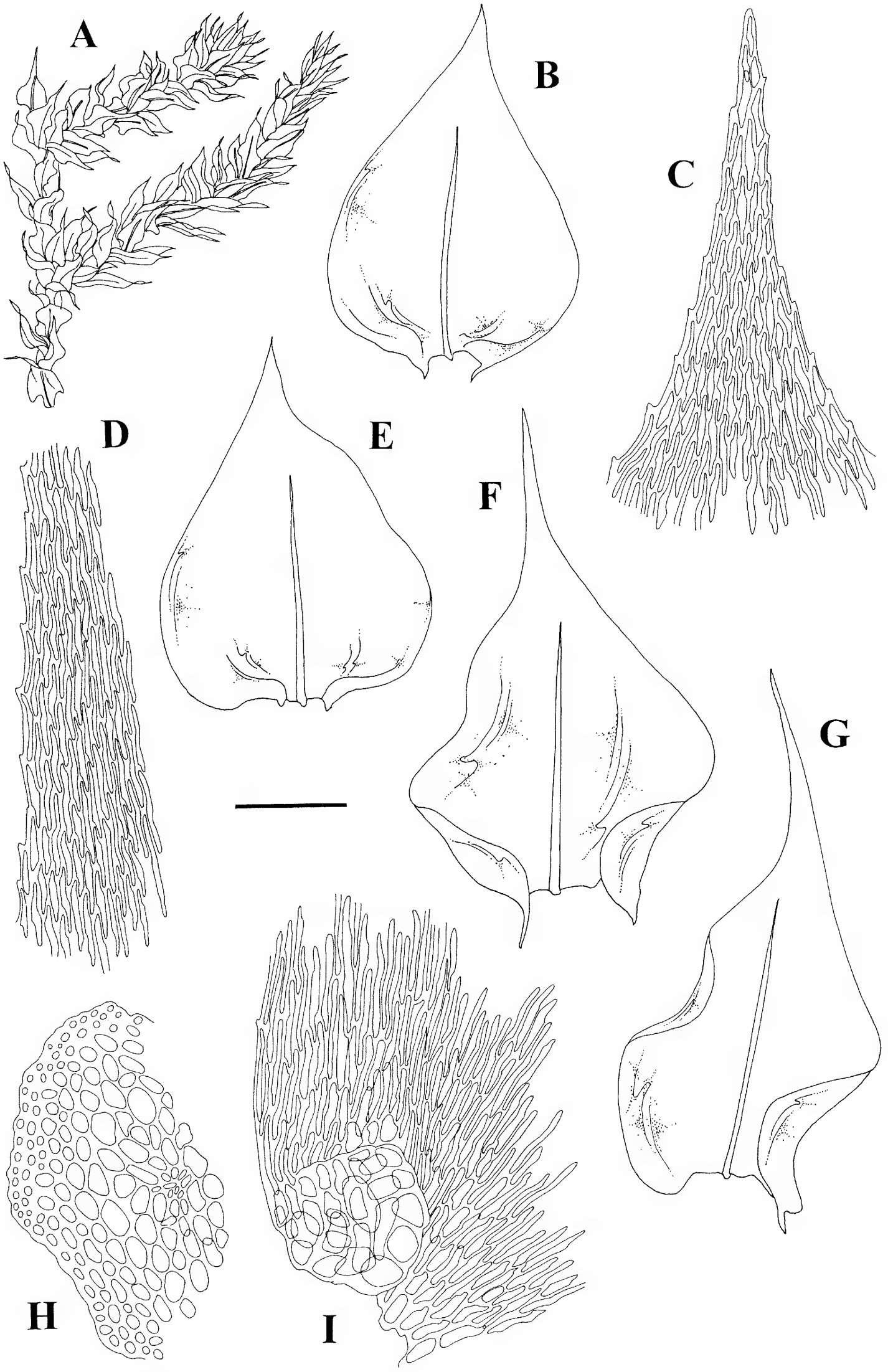
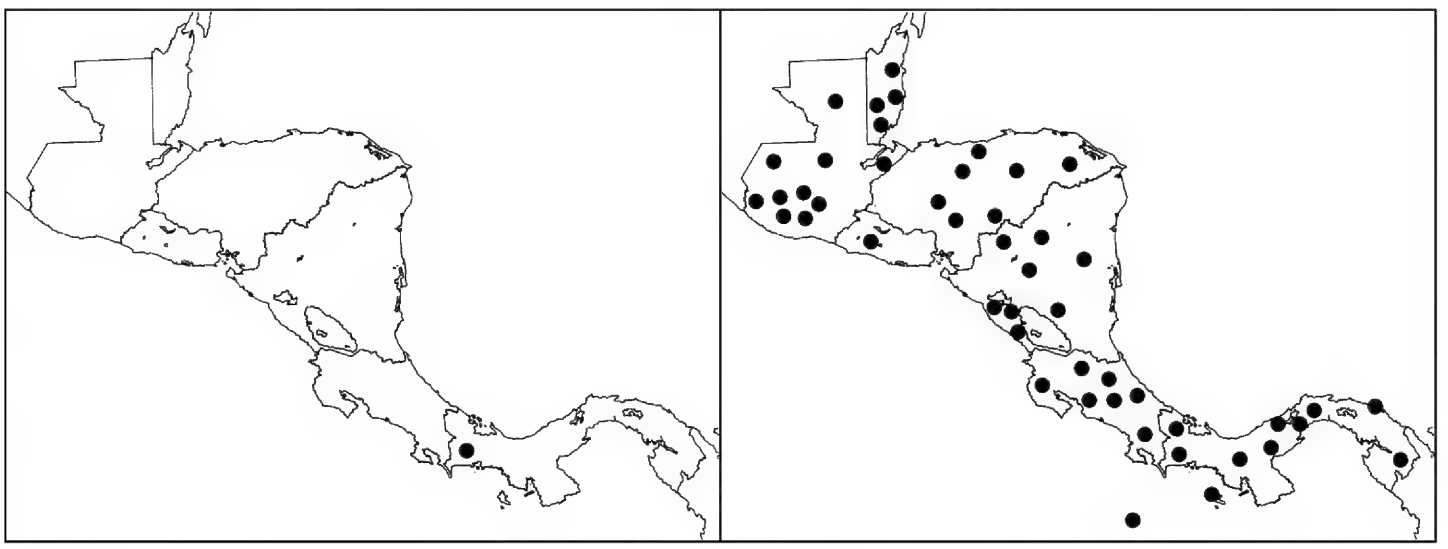


Figure 53. *Zelometeorium ambiguum*. A. Habit. B & E. Branch leaves. C. Leaf apex. D. Median leaf cells. F & G. Stem leaves. H. Stem in cross section. I. Basal and alar cells. Scale in mm: bar = 0.06 (C, D, H, I); bar = 0.4 (B, E–G); bar = 2.0 (A). A & H from *Grosse*; all other figure parts from *Wagner.*



Zelometeorium ambiguum *Zelometeorium patulum*

tangular, firm- to thick-walled, porose. Dioicous. Sporophytes not seen, description from Manuel (1977a). Capsules erect, emergent, elliptic to ovate, 1.3–1.8 × 0.9–0.95 mm; exothecial cells quadrate to rectangular, thick-walled, with oblique end-walls; opercula 1.0 mm long, shortly rostrate; exostome teeth linear, 440–630 µm long, papillose; endostome papillose, basal membranes low, segments 360–440 µm long, cilia absent. Spores 22.5–27.5 µm. Calyptrae mitrate, pilose, 1.8–1.9 mm long.

Illustrations. Manuel (1977a, Fig. 6). Figure 53.

Habitat. Corticolous or ramicolous on trees and shrubs; 50–2100 m (Manuel 1977a).

Distribution in Central America. PANAMA. Chiriquí: *M. Wagner*, 1858 (NY).

World range: Central America; Western and Southern South America, Brazil; West-Central Tropical Africa.

Zelometeorium ambiguum is a medium-sized species with strongly dimorphic stem and branch leaves. It is distinguished from all other members of the genus by its branch leaves that are erect (rarely somewhat spreading) and when dry have distinctly revolute basal margins. *Zelometeorium allionii* is a bigger species than *Z. ambiguum* and its branch leaves have a very well-developed sheathing leaf base. In *Z. recurvifolium* and *Z. patulum* the branch leaves are strongly spreading, squarrose, or squarrose-recurved.

The presence of *Z. ambiguum* in western Panama is remarkable since the nearest Neotropical station for the species is Bolivia. *Zelometeorium ambiguum* appears to be fairly common in southeastern Brazil; it is the only *Zelometeorium* species present in Paraguay, Uruguay, and Argentina and the only species of *Zelometeorium* in Africa.

3. *Zelometeorium patulum* (Hedw.) Manuel, J. Hattori Bot. Lab. 43: 118. 1977. *Hypnum patulum* Hedw., Sp. Musc. Frond. 279. 1801. *Neckera patula* (Hedw.) Schwägr., Sp. Musc. Frond. Suppl. 2(2)1: 43. 1826. *Pilotrichum patulum* (Hedw.) Brid., Bryol. Univ. 2: 795. 1827. *Meteorium patulum* (Hedw.) Dozy & Molk., Prodr. Fl. Bryol. Surinam. [Natuurk. Verh. Holl. Maatsch. Wetensch. Haarlem ser. 2, 10(3):] 21. 1854. *Isothecium patulum* (Hedw.) Mont. *ex* Dozy & Molk., Prodr. Fl. Bryol. Surinam. [Natuurk. Verh. Holl. Maatsch. Wetensch. Haarlem ser. 2, 10(3):] 21. 1854, invalid combination, in synonymy. *Meteoriopsis patula* (Hedw.) Broth., Nat. Pflanzenfam. I(3): 825. 1906. Protologue. Jamaica *s. loc.*, *Swartz s.n.* Types (see Manuel 1977a). G, lectotype; H, NY, S, isotypes.

Meteoriopsis patula var. *congesta* E. B. Bartram, Contr. U.S. Natl. Herb. 26: 95. 1928. Protologue. On tree, Los Ayotes, near Tilaran, Province of Guancaste, Costa Rica, altitude 600 to 700 meters, *Paul C. Standley and Juvenal Valerio*, January 21, 1926, *no. 45530*. Types. On tree, Los Ayotes, near Tilarán, Provincia de Guancaste, altitude 600–700 meters, *Paul C. Standley & Juvenal Valerio No. 45530*. Jan. 21, 1926 (FH, holotype; FH, NY, US, isotypes).

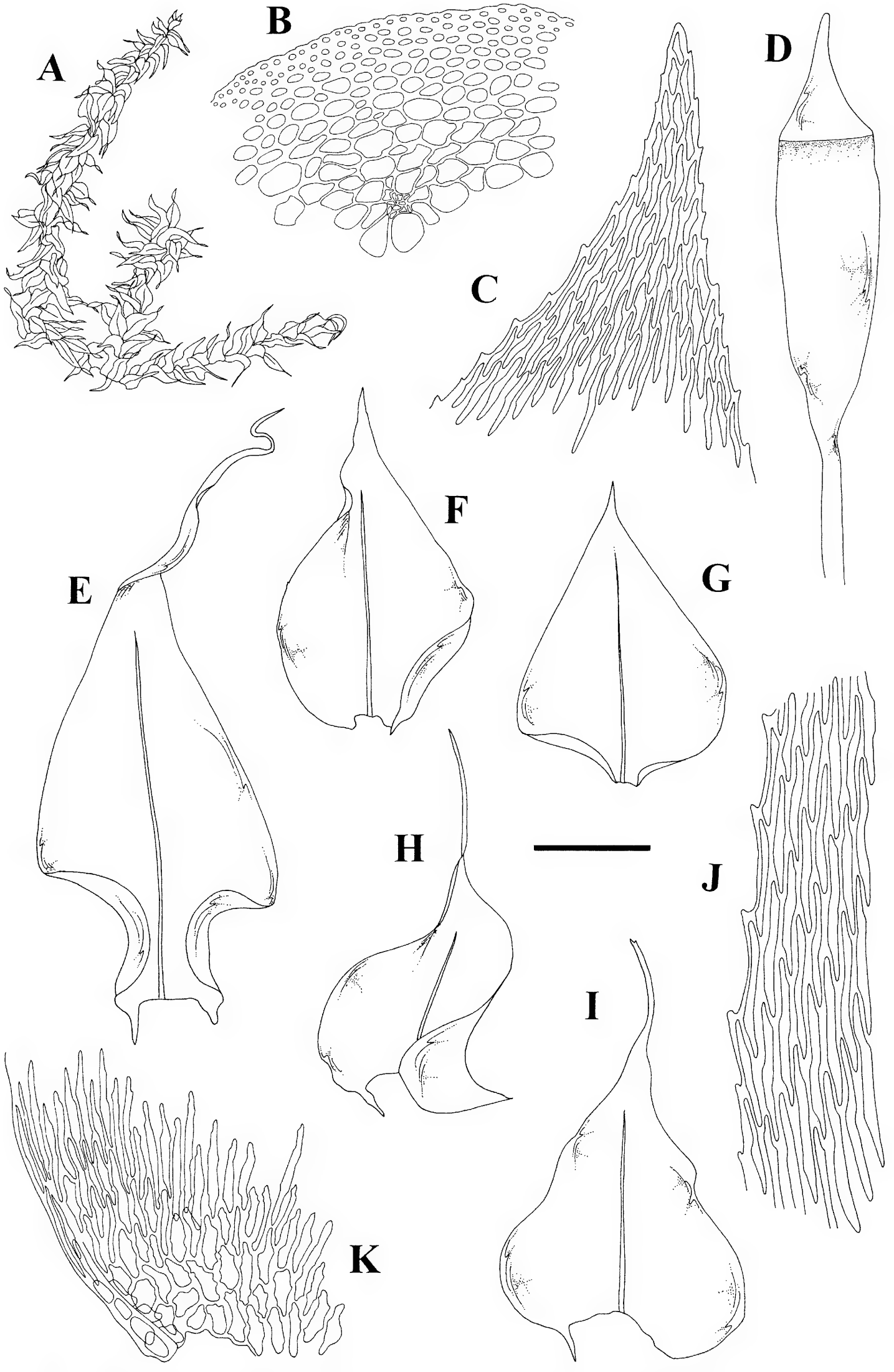


Figure 54. *Zelometeorium patulum*. A. Habit. B. Stem in cross section. C. Leaf apex. D. Seta, capsule, and operculum. E. Stolon leaf. F & G. Branch leaves. H & I. Stem leaves. J. Median leaf cells and margin. K. Basal and alar cells. Scale in mm: bar = 0.06 (C, J, K); bar = 0.08 (B); bar = 0.5 (E–I); bar = 0.9 (D); bar = 4.0 (A). All figure parts from *Allen 18048*.

Plants slender to medium-sized, green to yellow green, often in dense, creeping or pendent, epiphytic masses. Primary stems to 25 cm long; stems in cross section with 4–6 rows of small, thick-walled, yellow to red epidermal cells, cortical cells enlarged, thin-walled, hyaline, central strand small; irregularly branched, branches generally short, usually less than 1 cm long; rhizoids in dense groups, dark brown to blackish, smooth, not branched, from circular clusters of initials abaxial to the leaf insertions. Leaves trimorphic: stolon/primary stem leaves, secondary stem leaves, and branch leaves. Stolon/primary stem leaves erect, strongly clasping, ovate-lanceolate, 1.8–2.8 mm long; apices long-acuminate to piliferous, sometimes twisted; margins generally plane, subentire to serrulate; costae single, slender, tapering to the apex, commonly ending above midleaf, at times ending in a small spine; median cells linear-flexuose, 45–80 × 5–8 µm, firm-walled, not porose; alar cells weakly differentiated in excavate groups, somewhat porose. Secondary stem leaves erect-appressed, broadly ovate-lanceolate, to 2.0 mm long, otherwise similar to primary stem leaves. Branch leaves closely spaced, wide-spreading, squarrose, to squarrose-recurved, not clasping, ovate-lanceolate to ovate-acuminate, 0.7–1.8 mm long, short- to long-acuminate, cordate at base; margins plane or narrowly recurved below, subentire to serrulate above; costae single, slender, tapering to the apices, ending 1/2–3/4 the leaf length, at times ending in a small spine; median cells fusiform to linear-flexuose, 45–80 µm long, firm-walled; alar cells weakly differentiated, cells subquadrate, firm- to thick-walled, at times porose. Asexual reproduction occasionally by filiform branches from branch leaf axils. Dioicous. Setae red to dark red, twisted when dry, 1.5–3.5 mm long, smooth to somewhat roughened below capsules. Capsules exserted, erect, ellipsoid to cylindric, constricted at neck, 1.5–2.5 mm long; exothecial cells quadrate to oblate at the mouth, irregularly rectangular, below with thick vertical walls and thin horizontal walls; stomata superficial on neck; opercula 0.7–1.3 mm long, shortly rostrate; annuli rudimentary, of several rows of thick-walled cells; exostome teeth linear, yellow, papillose; endostome hyaline to light yellowish, smooth to lightly papillose, as long as the exostome, basal membranes low, segments linear, perforate below, cilia rudimentary or absent. Spores round, 15–22 µm, lightly papillose. Calyptrae mitrate, lobed, 1.5–2.0 mm long, densely hairy.

Illustrations. Hedwig (1801, Pl. 73 1–5); Dozy and Molkenboer (1854, Pl. 10); Bartram (1949, Fig. 122); Breen (1963, Pl. 107 5–7); Florschütz (1964, Fig. 103); Manuel (1977a, Fig. 8); Crum and Anderson (1981, Fig. 385); Churchill (1994, Fig. 28); Sharp *et al.* (1994, Fig. 548); Churchill and Linares (1995, Fig. 128 e–j); Duarte Bello (1997, Pl. 206); Buck (1998, Pl. 99 10–18); Buck (2003, Fig. 125). Figure 54.

Habitat. On tree roots, trunks, branches, twigs, and leaves, often pendent, also on logs, boulders, terrestrial on wet, shaded banks, and on roofs of old huts; 30–2000 m.

Distribution in Central America. BELIZE. Belize: *Gentle 1165* (F, FH, NY, US); Cayo: *Allen 18048* (BRH, MO); Stann Creek: *Gentle 2725* (F, FH, NY); Toledo: *Allen 18606* (BRM, MO). GUATEMALA. Alta Verapaz: *Steyermark 44857* (F, FH, MO); Chimaltenango: *Standley 62030* (F, FH); Guatemala: *Standley 58412a* (F, FH); Huehuetenango: *Steyermark 46561c* (F); Izabal: *Standley 72522* (F, FH); Petén: *Bartlett 12671* (FH, MO, NY, US); Quetzaltenango: *Standley 86688a* (F, FH, NY); Sacatepéquez: *Standley 88961b* (F, FH); San Marcos: *Croat 40815* (MO); Sololá: *Steyermark 47992* (F, FH, US). EL SALVADOR. San Salvador: *Carlson 429b* (F). HONDURAS. Atlántida: *Allen 17190* (MO, TEFH); Comayagua: *Standley & Chacón 6331* (F); El Paraíso: *Standley 16396* (F); Francisco Morazán: *Pilz & Pilz 1411* (MO); Gracias a Dios: *Wilson 693* (NY); Olancho: *Standley 18855* (F); Yoro: *Allen 13643* (MO, TEFH). NICARAGUA. Chontales: *Standley 9003* (F); Granada: *Almedo 1460b* (MO); Jinotega: *Stevens 16451b* (HNMN, MO, NY); Managua: *Standley 8408* (F); Matagalpa: *Stevens 9652* (MO); Nueva Segovia: *Moreno 13715* (MO); Rivas: *Granzow de la Cerda 1616* (DUKE, MO); Zelaya: *Schramm 1924* (FH, NY, US). COSTA RICA. Alajuela: *Alfaro 130* (F); Cartago: *Standley & Valerio 49594* (FH, US); Guanacaste: *Alfaro 85b* (F); Heredia: *Stevens 13504* (MO); Limón: *Daly 76* (MO); Puntarenas: *Liesner 1781* (MO), Cocos Island: *Gómez 4578* (MO); San José: *Alfaro 90* (F). PANAMA. Bocas del Toro: *Allen 5540* (MO, PMA); Canal Area: *Voth IV8b* (F, MO, PMA); Chiriquí: *Cornman 3009* (FH, MO, US); Coclé: *McPherson 7972G* (MO); Colón: *Crosby 10755* (MO, PMA); Darién: *Allen 8644* (MO); Panamá: *Bartlett & Lasser 16898* (FH, US); San Blas: *Allen 4982* (MO, PMA); Veraguas: *Crosby 10192* (MO), Isla de Coiba, *Méndez 65* (FH, NY).

World range: Southeastern U.S.A.; Mexico; Central America; Caribbean; Western, Northern, and Southern South America, Brazil.

Zelometeorium patulum is a common epiphytic species in Central America. It often grows in dense pendent masses from tree branches and twigs, but can also occur on boulders and on the ground. In Central America the latter habitats appear to be secondary for *Z. patulum*, indicating an ability to persist in shady, moist places after falling from epiphytic habitats. *Zelometeorium patulum* has two types of stem leaves (associated with different shoot types) and distinctly different branch leaves. As a result, the overall aspect of the plants varies greatly, depending upon the different types and predominance of leaves present. Stolon and stem leaves in *Z. patulum* are strongly clasping and long-acuminate to piliferous, while the branch leaves are closely spaced, spreading to squarrose from a somewhat erect base, and short- to long-acuminate. The costae in *Z. patulum* are slender and taper to the apices, and Buck (1998) noted the branch leaf costae sometimes end in a small spine. In Central America spined costae are present in both the stem and branch leaves.

Meteoridium remotifolium is often confused with *Z. patulum*, but it differs in several ways. In *M. remotifolium* the stem and branch leaves are similar in form, or only slightly different, they are widely spaced on the stems and branches, and they spread from the insertions. The leaf apices in *M. remotifolium* are consistently twisted when wet or dry, the margins are sharply serrate, and the alar cells are fairly well developed. There are some collections of *M. remotifolium* that have closely spaced branch leaves not obviously spreading from the insertions, and these collections are difficult to distinguish from *Z. patulum*. They can, however, be recognized as *M. remotifolium* by their similar stem and branch leaves that have twisted apices and sharply serrate margins.

The branch leaves of *Z. patulum* vary from spreading to squarrose, and their apices can be short- to long-acuminate. As a result of leaf variability in *Z. patulum*, Buck (1998) synonymized it with *Z. recurvifolium*. These two taxa can be very difficult to separate, and part of the confusion surrounding them may be due to Manuel (1977a) attributing spreading or squarrose leaves to *Z. recurvifolium* and squarrose to squarrose-recurved leaves to *Z. patulum*. In fact, *Z. recurvifolium* has squarrose to squarrose-recurved leaves while *Z. patulum* has wide-spreading to squarrose (rarely squarrose-recurved) leaves. *Zelometeorium recurvifolium* further differs from *Z. patulum* in having at least some more or less orbicular, apiculate branch leaves.

Manuel (1977a) considered the type sheet of *Hypnum patulum* (in G) to contain two distinct elements: one sterile, assignable to *Z. patulum*; the other with sporophytes, referable to *Z. recurvifolium*. Buck (1998) viewed the two elements as representing morphological extremes, *i.e.*, the *Z. patulum* form and the *Z. recurvifolium* form of his united species, both based on Swartz's type material from Jamaica. However, the mixed sheet can be traced to Schwägrichen's (1826) transfer of *Hypnum patulum* into *Neckera*, which was based on his examination of Jamaican and Brazilian material: "Ad radices et ramos arborum, versus summitates montium Jamaicae *Ol. Swartz*, fructificantem in Sierra de Estrella prope Mandiocam Augusto mense legit cl *Beyrich.*" In fact, these two elements in the Hedwig-Schwägrichen herbarium (G) represent type material of *Z. patulum* (Jamaica, *Swartz*) and *Z. recurvifolium* (Brazil, *Beyrich*).

4. *Zelometeorium recurvifolium* (Hornsch. *in* Mart.) Manuel, J. Hattori Bot. Lab. 43: 121. 1977. *Pilotrichum recurvifolium* Hornsch. *in* Mart., Fl. Bras. 1(2): 58. 1840. *Meteorium recurvifolium* (Hornsch. *in* Mart.) Mitt., J. Linn. Soc., Bot. 12: 444. 1869. *Meteoriopsis recurvifolia* (Hornsch. *in* Mart.) Broth., Nat. Pflanzenfam. I(3): 825. 1906. Protologue. Brazil. Ad corticem arborum in Serra d'Estrella, Augusto, cum fructibus maturis: *Beyrich.* Types (see Manuel 1977a). BM, lectotype; BM, G, NY, isolectotypes.

Plants slender to medium-sized, green to yellow green, often in dense, creeping or pendent, epiphytic masses. Primary stems to 30 cm long, irregularly branched, branches short to medium-sized, to 2 cm long; stems in cross section with 4–6 rows of small, thick-walled, yellow to red epidermal cells, cortical cells enlarged, firm-walled, hyaline to yellowish, central strand small; rhizoids in dense groups, dark brown to blackish, smooth, not branched, from circular clusters of initials abaxial to the leaf insertions. Leaves trimorphic: stolon/primary stem leaves, secondary stem leaves, and branch leaves. Stolon/primary stem leaves erect, strongly clasping, ovate-lanceolate, 1.5–2.5 mm long;

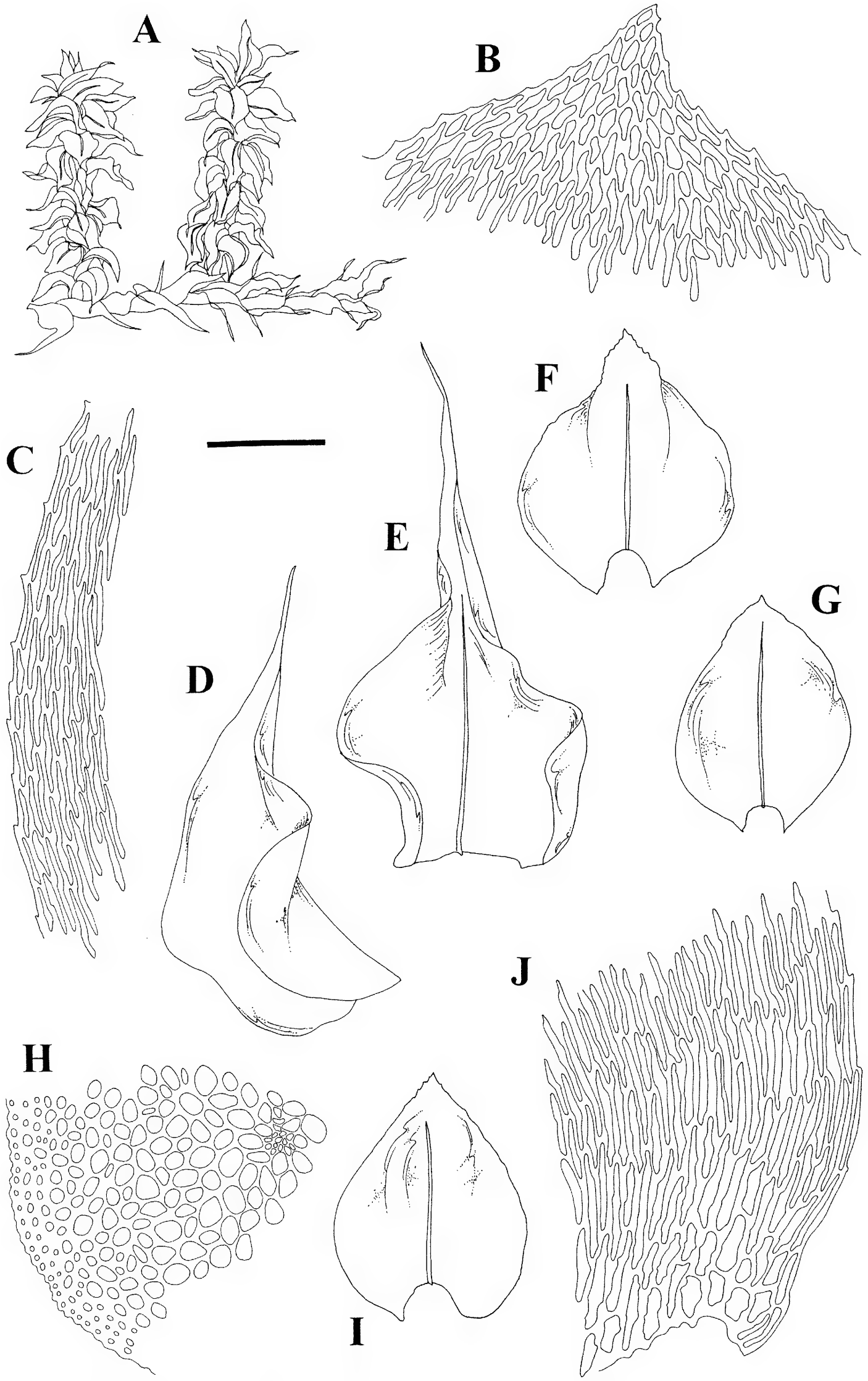
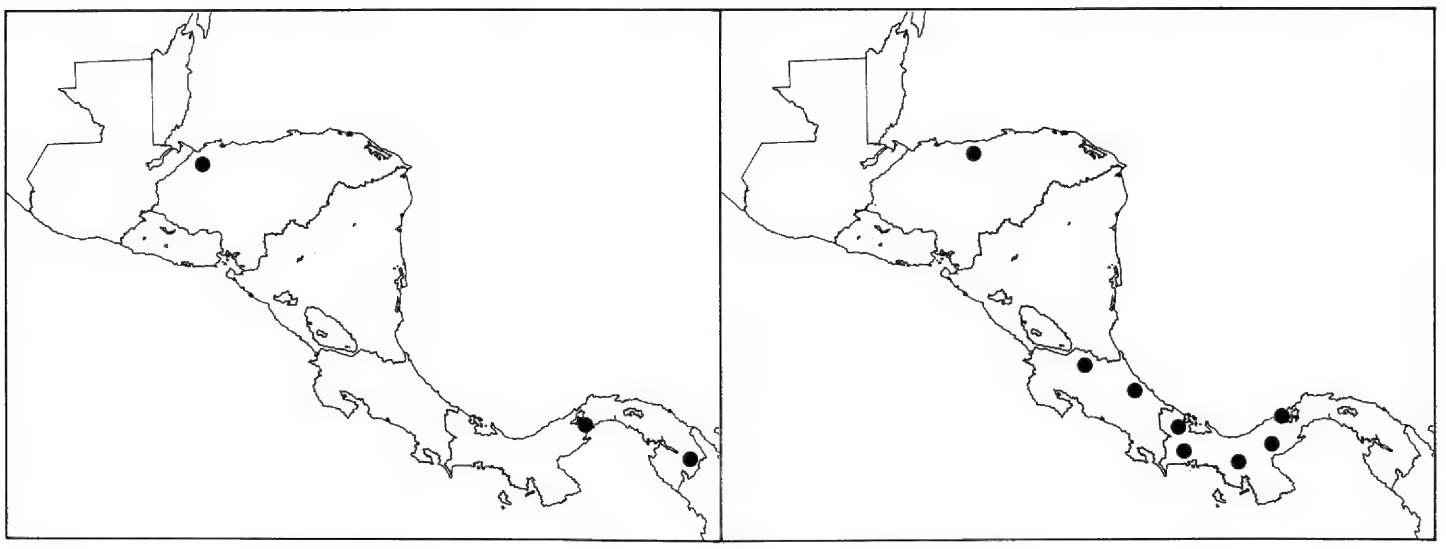


Figure 55. *Zelometeorium recurvifolium*. A. Habit. B. Leaf apex. C. Median leaf cells and margin. D & E. Stem leaves. F, G & I. Branch leaves. H. Stem in cross section. J. Basal and alar cells. Scale in mm: bar = 0.06 (B, C, J); bar = 0.08 (H); bar = 0.5 (D–G, I); bar = 2.5 (A). All figure parts from *Allen 14088*.



Zelometeorium recurvifolium *Lepyrodontopsis trichophylla*

apices long-acuminate to piliferous, sometimes twisted; margins generally plane, subentire; costae single, slender, tapering to the apex, commonly ending above midleaf; median cells linear-flexuose, 45–80 × 5–7 µm, firm-walled, often porose; alar cells weakly differentiated. Secondary stem leaves erect-appressed, broadly ovate-lanceolate, to 2.0 mm long, otherwise similar to primary stem leaves. Branch leaves closely spaced, squarrose to squarrose-recurved, not clasping, broadly ovate to orbicular, 0.8–1.5 mm long, short-acuminate to apiculate; margins plane, serrulate; costae single, slender, tapering to the apex, ending 1/2–3/4 the leaf length; median cells fusiform to linear-flexuose, 35–70 µm long, firm-walled, not porose; alar cells weakly differentiated, subquadrate, firm- to thick-walled, at times porose. Dioicous. Perichaetia lateral on stems and branches. Setae red to dark red, twisted when dry, 1.5–2.5 mm long, smooth to somewhat roughened below capsules. Capsules exserted, erect, cylindric, constricted at neck, 1.5–2.3 mm long; exothecial cells quadrate to oblate at the mouth, irregularly rectangular, below with thick vertical walls and thin horizontal walls; stomata superficial on neck; opercula 1.0 mm long, shortly rostrate; annuli rudimentary, of several rows of thick-walled cells; exostome teeth linear, yellow, papillose; endostome hyaline to light yellowish, lightly papillose, 2/3 the exostome length, basal membranes low, segments linear, perforate below, cilia rudimentary or absent. Spores round, 14–24 µm, lightly papillose. Calyptrae mitrate, lobed, 1.5 mm long, densely hairy.

Illustrations. Schwägrichen (1826, Pl. 165, as *Neckera patula*); Manuel (1977a, Fig. 9). Figure 55.

Habitat. On twigs, vines, leaves, and fallen branches; 400–1500 m.

Distribution in Central America. HONDURAS. Cortés: *Allen 14088* (MO, TEFH). PANAMA. Canal Area: *Cornman 3033* (F, MO); Darién: *Williams 1067* (F, FH, NY).

World range: Central America; Western and Northern South America, Brazil.

Zelometeorium recurvifolium is a mostly South American species known from only a few Central American collections. The species has broadly ovate to orbicular branch leaves that are consistently squarrose to squarrose-recurved and either short-acuminate or apiculate. *Zelometeorium recurvifolium* is very close to *Z. patulum*. Most collections of *Z. patulum* have wide-spreading to squarrose rather than squarrose-recurved branch leaves, and this enables them to be separated from *Z. recurvifolium*. There are, however, some collections of *Z. patulum* with branch leaves as squarrose-recurved as those of *Z. recurvifolium.* These collections can be distinguished from *Z. recurvifolium* only by their narrower branch leaves that are never apiculate. The leaves in all species of *Zelometeorium* are extremely variable in form, and because of this variability Buck (1998) synonymized *Z. patulum* and *Z. recurvifolium*. In the present treatment *Z. recurvifolium* is maintained, based on the combination of its squarrose-recurved branch leaves that are predominantly broadly ovate to orbicular and apiculate.

Manuel (1977a) noted that the type sheet of *Hypnum patulum* (in G) consisted of two distinct elements: one sterile and assignable to *Z. patulum*, the other with sporophytes and referable to *Z. re-*

curvifolium. This mixture can be traced to Schwägrichen's (1826) transfer of *Hypnum patulum* into *Neckera*, which was based on his examination of Jamaican and Brazilian material: "Ad radices et ramos arborum, versus summitates montium Jamaicae *Ol. Swartz*, fructificantem in Sierra de Estrella prope Mandiocam Augusto mense legit cl *Beyrich.*" These two elements in the Hedwig-Schwägrichen herbarium (G) represent not only type material of *Z. patulum* (Jamaica, *Swartz*) but also *Z. recurvifolium* (Brazil, *Beyrich*).

Excluded taxa, or types not seen

Cryptopapillaria penicillata (Dozy & Molk.) M. Menzel, Willdenowia 22: 182. 1992. *Meteorium penicillatum* Dozy & Molk., Prodr. Fl. Bryol. Surinam. [Natuurk. Verh. Holl. Maatsch. Wetensch. Haarlem ser. 2, 10(3):] 45. 1854. *Papillaria penicillata* (Dozy & Molk.) Broth., Nat. Pflanzenfam. I(3): 815. 1906. Protologue. In Venezuela, ad arbores in sylvis juxta Rio del Tuy, unde benevole misit vir nobiliss *van Lansbergen*. Type (see Menzel 1992). L, holotype.

Cryptopapillaria penicillata is a South American species that has been widely confused with *Meteorium laevifolium*. For example, all Neotropical material at MO named *C. penicillata* is actually *M. laevifolium.* Buck (1998) tentatively synonymized the two species, but they are not very similar. In *C. penicillata* the leaves are loosely erect when dry, while those of *M. laevifolium* are smoothly imbricate. Furthermore, the leaf apices in *M. laevifolium* are plane, while those of *C. penicillata* are twisted in a way similar to the twisted leaf apices of *Toloxis imponderosa*. Most importantly, the leaf cells in *C. penicillata* are pluripapillose, with the papillae arranged over the cell walls. In *M. laevifolium* the leaf papillae are centered over the cell lumina. The sporophytes of *C. penicillata* also differ from those of *M. laevifolium* in having immersed capsules, very long, linear-lanceolate perichaetial leaves, and mitrate calyptrae. *Toloxis imponderosa* differs from *C. penicillata* in having more widely spaced, slenderly lanceolate-triangular leaves. Furthermore, as with *M. laevifolium*, the leaf cell papillae in *T. imponderosa* are arranged over the cell lumina.

Within Central American Meteoriaceae, the only other species with pluripapillose leaf cells in which the papillae are centered over the cell walls rather than the lumina is *Trachypus bicolor* var. *viridulus*. That taxon differs from *C. penicillata* in having much narrower, lanceolate to ovate lanceolate leaves that are erect-spreading when dry. In addition, the leaves of *T. bicolor* var. *viridulus* are not or weakly auriculate and have long-hexagonal to linear leaf cells.

Papillaria warszewiczii Müll. Hal., Bull. Herb. Boissier 5: 205. 1897. Protologue. Guatemala. Sine loco natali misit hortulanus *Warszewicz* ante annos multos.

Type material was not examined. From its description it appears to be *Meteorium deppei*.

Aerobryopsis martinicensis (Broth.) Spessard-Schueth and ***A. longissima*** (Dozy & Molk.) M. Fleisch.

Spessard-Schueth (1994a) reported *Aerobryopsis martinicensis* and *A. longissima* from Central America. However, all Central American material annotated by Spessard-Schueth as these species is *Floribundaria flaccida* or *Meteorium deppei*.

LEMBOPHYLLACEAE

Lembophyllaceae Broth., Nat. Pflanzenfam. I(3): 863. 1906.

Plants slender, medium-sized, or large, light green, yellow green, reddish yellow, or brownish green, in loose mats often with pendent strands. Stolons present or absent. Primary stems often stipitate, irregularly branched, branch and stem tips occasionally flagelliform; stems and branches in cross section with sclerodermis, enlarged, firm-walled cortex, central strand absent (rarely present); paraphyllia absent; pseudoparaphyllia absent or occasionally filamentous to subfoliose, scale leaves present; rhizoids generally on parts of the stems and branches in contact with the substrate, from circular clusters of initials abaxial to the leaf insertions, mostly not branched. Leaves monomorphic or dimorphic, when dimorphic stolon and stipe leaves of one form, stem and branch leaves of another, leaves unranked or branch leaves seriately ranked; costae absent or occasionally short and double or single; leaf cells long-flexuose, smooth; alar cells strongly or weakly developed. Asexual reproduction by slender, deciduous branchlets with microphyllous leaves, short branches with deciduous leaves, or uniseriate, septate propagula arising at the abaxial side of the leaf insertions or clustered around branch primordia. Dioicous. Vaginulae moderately to densely hairy. Setae short or long, smooth below and papillose above or papillose-roughened throughout. Capsules exserted; stomata superficial; opercula obliquely long-rostrate; annuli rudimentary; peristome diplolepideous, yellowish white; exostome teeth linear, dorsal (outer) surface lightly horizontally striate at base, smooth or finely papillose above, trabeculae weakly developed on both sides; endostome nearly as long as exostome, basal membranes low, segments filamentous, narrowly perforate, not keeled, cilia rudimentary or absent. Spores uni- or bimodal, at times massive. Calyptrae cucullate, smooth or hairy.

The Lembophyllaceae were established by Brotherus (1906a, 1907b) for four genera with a stipitate habit, mostly well-formed, hypnaceous peristomes, and usually well-differentiated alar cells. The family concept has since undergone considerable change as the number of included genera has expanded or contracted (Fleischer 1908; Brotherus 1925; Andrews 1952; Robinson 1975; Buck & Vitt 1986; Crum 1991; Buck 1994a; Tangney 1997; Buck & Goffinet 2000; Goffinet & Buck 2004), and there is presently no consensus on its generic composition. Tangney (1997) in a generic revision of the Lembophyllaceae restricted them to *Camptochaete* Reichardt, *Fallaciella* Crum, *Fifea* Crum, *Lembophyllum* Lindb., and *Weymouthia* Broth. This alignment of genera is supported by sporophytic and gametophytic evidence as well as biogeography. Quandt and Huttunen (2004) provided molecular evidence supporting the placement of these genera, along with *Neobarbella* Nog., in the Lembophyllaceae. Their study also indicated the Lembophyllaceae were closely related to the Neckeraceae. The inclusion of *Neobarbella* in the Lembophyllaceae removes the peristomial cohesion of the group, since that genus has a leucodontoid rather than hypnoid peristome. *Pilotrichella* and *Lepyrodontopsis* are here included in the family. As treated here the Lembophyllaceae are characterized by: (1) stoloniferous primary stems; (2) often stipitate secondary stems; (3) generally ovate-oblong, concave leaves with inflexed upper leaf margins; (4) differentiated alar cells; (5) linear-flexuose median leaf cells; (6) weak, short double costae, often variably expressed or absent.

1. Stem central strand present; leaves linear to slenderly long-lanceolate, plicate; basal margins with prominent, wide-spreading teeth . . . . . 1. *Lepyrodontopsis*
1. Stem central strand absent; leaves ovate, obovate to oblong-obovate, at times panduriform, smooth; basal margins entire or serrulate . . . . . 2. *Pilotrichella*

1. *Lepyrodontopsis* Broth., Nat. Pflanzenfam. (ed. 2) 11: 358. 1925.

Plants small and slender to medium-sized in glossy, lax to dense, silky mats, at times pendent. Primary stems creeping, with erect to imbricate distantly spaced leaves; stems in cross section with sclerodermis, enlarged cortical cells, and small central strand; paraphyllia absent; pseudoparaphyllia filamentous to subfoliose; rhizoids red brown, roughened, irregularly branched from small clusters of initials abaxial to the leaf insertions; leaves erect to imbricate, distantly spaced. Secondary stems irregularly spaced, erect to pendent, not branched but branch primordia present, more or less complanate-foliate, often becoming flagellate or transformed to stoloniferous stems; leaves closely spaced,

erect-spreading to wide-spreading, linear to slenderly long-lanceolate, plicate, long-acuminate to hair-pointed, concave, subauriculate at base, not decurrent; margins serrate to serrulate throughout with prominent, wide-spreading teeth at base, plane to narrowly recurved below; costae absent; cells linear, smooth, thick-walled, conspicuously porose; alar cells weakly developed, with 2–5 short-rectangular to subquadrate, porose cells. Asexual reproduction by deciduous flagellate branches, with microphyllous leaves or brown, papillose, uniseriate, septate propagula arising from rhizoidal initials at the abaxial side of the leaf insertions or clustered around branch primordia. Dioicous. Setae elongate, smooth. Capsules erect, ovoid-cylindrical; exothecial cells oblate below the mouth, short-rectangular below, not collenchymatous; stomata on neck; opercula obliquely long-rostrate; annuli rudimentary, of 2–3 rows of firm-walled cells; peristome diplolepideous; exostome teeth brown, narrowly triangular, papillose, weakly trabeculate; endostome paler, papillose, nearly as long as the exostome, basal membranes short, segments narrow, keeled, not or scarcely perforate, cilia rudimentary or absent. Calyptrae cucullate, naked, smooth or slightly roughened above.

Lepyrodontopsis is a monospecific genus found only in the Neotropics. The genus has creeping primary stems, a weak central strand, and filamentous to subfoliose pseudoparaphyllia. In the past, plants of *Lepyrodontopsis* have been interpreted as having more or less erect branches from a creeping stem. The erect structures, however, have arrested branch primordia with filamentous pseudoparaphyllia. As a result, the genus is here interpreted as having creeping primary stems, erect secondary stems, and no branches. Its leaves are narrowly lanceolate to linear, plicate, ecostate, with sharply serrate to serrulate margins, long porose cells, and weakly differentiated alar cells. *Lepyrodontopsis* is dioicous. Its sporophytes have erect capsules, long-rostrate opercula, and a reduced diplolepideous peristome consisting of narrow, papillose exostome teeth and endostomes with short basal membranes, narrow segments, and rudimentary or absent cilia.

Mitten (1869) associated this genus with *Lepyrodon* (as *Lepyrodon trichophyllus*), and the two genera share the features of lanceolate to linear leaves, linear-vermicular, incrassate and porose leaf cells, weakly differentiated alar cells, a dioicous sexual condition, erect, cylindrical capsules, obliquely rostrate opercula, and cucullate calyptrae. *Lepyrodon* differs from *Lepyrodontopsis* in having weakly costate leaves, rhizoidal initials from around branch buds or in leaf axils, and a very reduced, mostly single, endostomial peristome. Müller (1896) related the genus to the Brachytheciaceae (as *Palamocladium trichophyllum*). The leaves of *Palamocladium* and *Lepyrodontopsis* are similar in shape, as are their leaf cells and leaf marginal serrations. *Palamocladium*, however, has strongly costate leaves, better-developed alar cells, cross-striate exostome teeth, and no filamentous pseudoparaphyllia. Britton (1913) allied the genus to the Sematophyllaceae (as *Clastobryum trichophyllum*), due to its ecostate leaves and the presence in its leaf axils of numerous red, filamentous gemmae. The near absence of alar cell development in *Lepyrodontopsis* rules out a placement for the genus in the Sematophyllaceae. The genus has recently been placed in the Meteoriaceae (Buck 1998; Buck & Goffinet 2000; Goffinet & Buck 2004). Quandt and Huttunen (2004) and Huttunen *et al.* (2004), on the basis of molecular (chloroplast and nuclear DNA) and morphological analyses, concluded that *Lepyrodontopsis* was not associated with either the Meteoriaceae or Brachytheciaceae but rather occupied a basal, but unsupported, position within a Lembophyllaceae–Neckeraceae clade.

The name *Lepyrodontopsis* combines the generic name *Lepyrodon* with the Greek *opsis* (aspect or appearance).

Lepyrodontopsis trichophylla (Hedw.) Broth., Nat. Pflanzenfam. (ed. 2) 11: 358. 1925. *Hypnum trichophyllum* Sw. *ex* Hedw., Sp. Musc. Frond. 274. 71. 1801. *Neckera trichophylla* (Hedw.) Sw., Fl. Ind. Occ. 3: 1798. 1806. *Anomodon trichophyllum* (Hedw.) Fuernr., Flora 12(2) Erg.: 49. 1829. *Lepyrodon trichophyllus* (Hedw.) Mitt., J. Linn. Soc., Bot. 12: 422. 1869. *Leucodon trichophyllus* (Hedw.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 218. 1877. *Palamocladium trichophyllum* (Hedw.) Müll. Hal., Flora 82: 466. 1896. *Orthothecium trichophyllum* (Hedw.) M. Fleisch. *in* Broth., Nat. Pflanzenfam. I(3): 1231. 1909. *Clastobryum trichophyllum* (Hedw.) E. Britton, Bull. Torrey Bot. Club 40: 669. 1913. Protologue. In insulis Jamaicae legit et communicavit D. O. Swartz. Type. *Swartz* (BM, isotype).

Taxicaulis andino-subulatus Müll. Hal., Flora 83: 340. 1897. Protologue. [Venezuela] Cumbre de St. Hilario, *Goebel*.

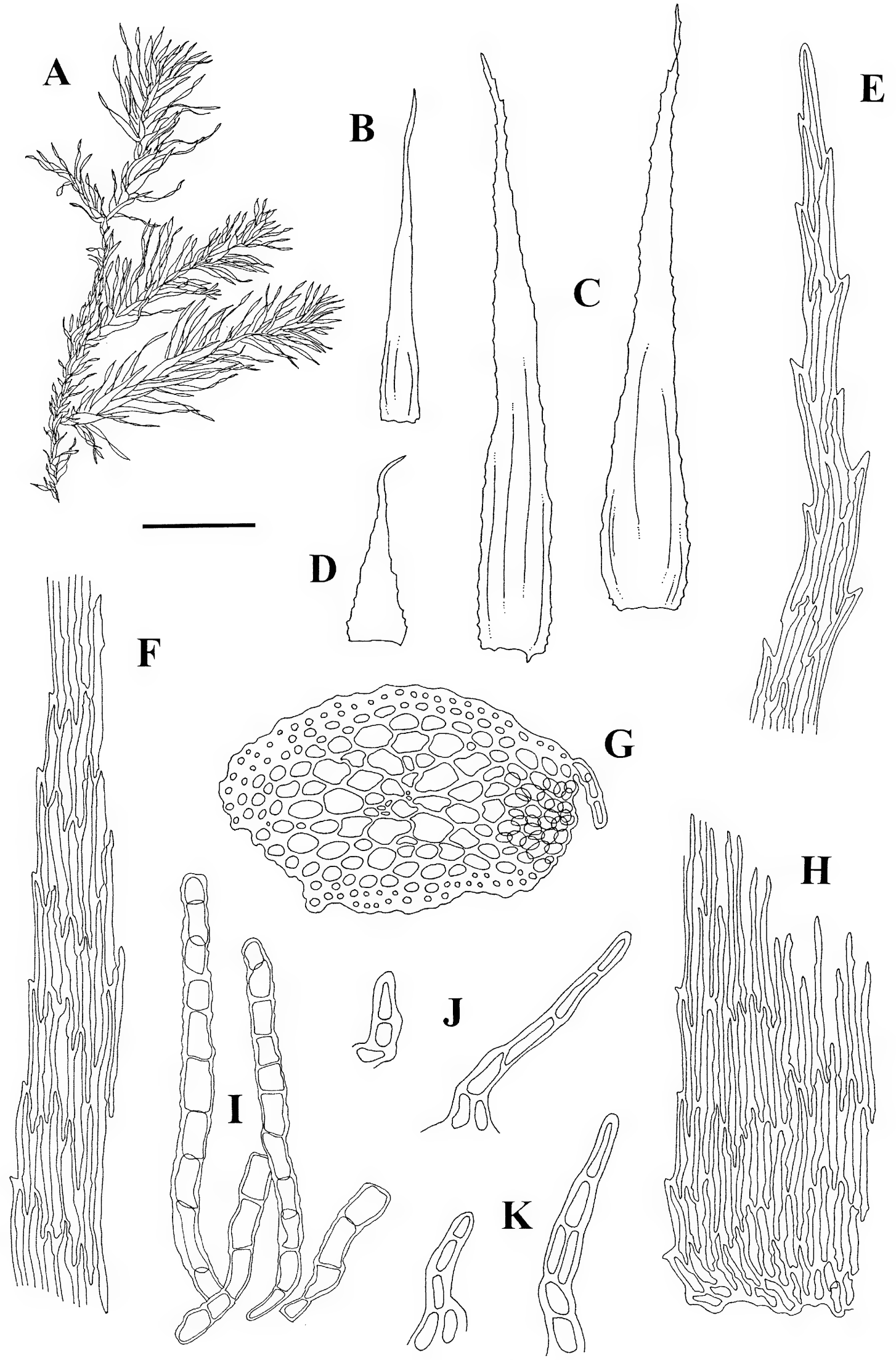


Figure 56. *Lepyrodontopsis trichophylla*. A. Habit. B & D. Primary stem leaves. C. Secondary stem leaves. E. Leaf apex. F. Median leaf cells. G. Stem in cross section. H. Basal and alar cells. I. Gemmae. J & K. Pseudoparaphyllia. Scale in mm: bar = 0.04 (J, K); bar = 0.05 (E–H); bar = 0.06 (I); bar = 0.4 (B–D); bar = 2.6 (A). All figure parts from *Allen 17222*.

Palamocladium trichophyllum var. *subtilis* Müll. Hal., Hedwigia 37: 240. 1898. *Lepyrodon trichophyllus* var. *subtilis* (Müll. Hal.) Paris, Index Bryol. Suppl. 226. 1900. Protologue. Venezuela, Cumbre de St. Hilario, *C. Goebel* Oct 1890; St. Domingo, in monte Isabel de la Torre, 600 m alt., Julio 1887, *Egers in Hb Krug & Urban*.

Lepyrodon trichophyllus fo. *robustior* Besch., Ann. Sci. Nat., Bot. sér. 6, 3: 224. 1876. *Lepyrodon trichophyllus* var. *robustior* Besch. *ex* Paris, Index Bryol. 800. 1897, invalid name, error for *L. trichophyllus* fo. *robustior*. Based on: Guadeloupe, la Découverte, sur les troncs pourris (*Husnot, no. 183*, sub *Meteorio sericeo* Sch.), (BM). — Martinique, montagne Pelée (*Husnot*; *Plée* [sic], *no. 869* in herb. Mus. Paris, coll. Montagne.

Meteorium sericeum Schimp. *in* Besch., Ann. Sci. Nat., Bot. sér. 6, 3: 224. 1876, invalid name, lacks a description. Based on Guadeloupe, la Découverte, sur les troncs pourris (*Husnot*, *n*^{o} *183*) (BM).

Plants small and slender to medium-sized, in green to yellow green, glossy, lax to dense, silky mats, at times pendent. Primary stems creeping to 10 cm long with erect to imbricate, distantly spaced leaves; stems in cross section with sclerodermis of 1–2 rows of small, reddish yellow, thick-walled cells, cortical cells enlarged, yellowish to hyaline, thin-walled, central strand small; paraphyllia absent; pseudoparaphyllia filamentous to subfoliose; rhizoids red brown, roughened, irregularly branched from small clusters of initials abaxial to the leaf insertions; leaves erect to imbricate, distantly spaced, 1.0–2.0 mm long. Secondary stems irregularly spaced, erect or pendent, 1–2 cm long, not branched but branch primordia present, often becoming flagellate, or transformed to stoloniferous stems, more or less complanate-foliate; leaves closely spaced, erect-spreading to wide-spreading, 1.6–4.0 mm long, linear to slenderly long-lanceolate, plicate, long-acuminate to hair-pointed, concave, subauriculate at base, not decurrent; margins serrate to serrulate throughout, with prominent, wide-spreading teeth at base, plane to narrowly recurved below; costae absent; cells linear, to 100 × 4 µm at base, smooth, thick-walled, conspicuously porose; alar cells weakly developed, of 2–5 short-rectangular to subquadrate, porose cells. Asexual reproduction by deciduous flagellate branches with microphyllous leaves and brown, papillose, uniseriate, septate propagula either arising from rhizoidal initials at the abaxial side of the leaf insertions or clustered around branch primordia. Dioicous. Sporophytes unknown from Central America, not seen, description from Britton (1913) and Buck (1998). Setae elongate, straight or flexuose, smooth, red, 15–25 mm long. Capsules erect, ovoid-cylindrical, 2–3 mm long; exothecial cells oblate below the mouth, short-rectangular below, not collenchymatous; stomata on neck; opercula obliquely long-rostrate, 1 mm long; annuli rudimentary, of 2–3 rows of firm-walled cells; peristome diplolepideous; exostome teeth brown, narrowly triangular, papillose, weakly trabeculate; endostome paler, papillose, nearly as long as the exostome, basal membranes short, segments narrow, keeled, not or scarcely perforate, cilia rudimentary or absent. Spores 5–16 µm, round, lightly papillose. Calyptrae cucullate, naked, smooth or slightly roughened above, 2–3 mm long.

Illustrations. Hedwig (1801, Pl. 71 1–3); Brotherus (1906b, Fig. 580 H–L); Britton (1913, Pl. 25); Brotherus (1925, Fig. 516 H–L); Crum and Steere (1957, Fig. 44); Duarte Bello (1997, Pl. 207); Buck (1998, Pl. 100 8–17); Gradstein *et al.* (2001, Fig. 154 I–M). Figure 56.

Habitat. On tree trunks, pendent from branches, roots, tree fern stems, stumps, rotting logs, soil, rocks, and vertical cliff faces; near sea level to 1600 m.

Distribution in Central America. HONDURAS. Atlántida: *Allen 17222* (MO). COSTA RICA. Alajuela: *Lyon 629* (CR, MO); Limón: *Crosby 3678* (CR, MO, TENN). PANAMA. Bocas del Toro: *Allen 5803* (MO, PMA); Chiriquí: *Chickering* (FH); Coclé: *Crosby 4433* (MO); Colón: *Crosby 10774* (MO); Veraguas: *Crosby 10131* (MO, PMA).

World range: Central America; Caribbean; Western and Northern South America.

Plants of *Lepyrodontopsis trichophylla* can be exceedingly slender or medium in size. Typically, the plants grow epiphytically; however, they also can be found on soil, rocks, or rock outcrops. The long, narrowly acuminate or linear leaves of *L. trichophylla* are plicate, with sharply serrulate to serrate margins and linear, smooth, thick-walled, porose cells. The best distinguishing leaf features of *L. trichophylla* are its absolutely ecostate leaves and basal leaf margins that bear large, often recurved teeth. The sporophytes of *L. trichophylla* are not known from Central America and are rarely encountered anywhere else in its range. The species reproduces asexually by means of deciduous, flag-

ellate branches and uniseriate propagula that are restricted to the flagellate branches. The uniseriate propagula originate from two places: transformed rhizoidal initials abaxial to the leaf insertions and in association with arrested branch primordia in the leaf axils. Regardless of their origin, the propagula in *L. trichophylla* are more or less similar in form.

Palamocladium leskeoides (Hook.) E. Britton can be very similar in aspect to *Lepyrodontopsis trichophylla*, and both species have basal margins with recurved teeth. It differs from *L. trichophylla* in having strongly costate leaves and exostome teeth that are cross-striate at base.

2. *Pilotrichella* (Müll. Hal.) Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 222. 1872. *Neckera* Hedw. subsect. *Pilotrichella* Müll. Hal., Syn. Musc. Frond. 2: 129. 1850.

Pilotrichella sect. *Turgidella* Müll. Hal., Flora 82: 464. 1896, invalid name, lacks a description.
Pilotrichella sect. *Gastrella* Müll. Hal., Flora 82: 464. 1896, invalid name, lacks a description.
Pilotrichella sect. *Eupilotrichella* Besch. *ex* Broth., Nat. Pflanzenfam. I(3): 811. 1906, illegitimate name (Art. 21.3, McNeill *et al.* 2006).

Plants small, medium-sized, or large, dull, light green, green, yellow green, reddish yellow, or golden brown, in loose or stiff mats, often with pendent strands. Primary stems creeping, secondary stems arising irregularly from the primary stems or primary stems transformed at the tips into secondary stems, often pendent, irregularly branched; stems and branches in cross section with sclerodermis, firm-walled cortical cells, central strand absent; paraphyllia absent; pseudoparaphyllia absent, scale leaves present; rhizoids on the parts of stems in contact with the substrate, from circular clusters of initials abaxial to the leaf insertions, dark red, smooth to finely roughened, mostly not branched; leaves smaller but not different in form or structure from secondary stem and branch leaves; axillary hairs numerous; basal cells short, subquadrate, upper cells long cylindrical, all cells reddish. Secondary stem and branch buds short and swollen or narrowly elongate and terete. Leaves not ranked, turgid when dry, erect-spreading, spreading or wide-spreading when wet, concave, ovate, oblong-ovate, obovate, or ovate-deltoid, at times panduriform, somewhat clasping at base, broadly rounded, acute or acuminate, mucronate, acuminate, cuspidate or hair-pointed, leaf tips reflexed or straight, variously auriculate; margins broadly incurved above, at times meeting or overlapping at upper margins, entire below, variously serrulate directly below the apex; costa absent; leaf cells linear-flexuose, porose or occasionally smooth above, porose at base; alar cells strongly differentiated in bulging, excavate groups, subquadrate to short-rectangular, usually dark red or reddish orange. Branch and stem tips occasionally flagelliform. Asexual reproduction sometimes by slender branchlets with microphyllous leaves or short branches with deciduous leaves. Dioicous. Perigonia gemmate, lateral on secondary stems and branches; perichaetia on short lateral branches; vaginulae of fertilized perichaetia densely hairy. Setae elongate, red, smooth below and papillose above or papillose-roughened throughout. Capsules exserted, erect, ovoid to short cylindrical; exothecial cells subquadrate to irregularly subrectangular, firm-walled; stomata superficial, on neck; opercula long-rostrate; annuli rudimentary; peristome diplolepideous; exostome teeth yellowish white, lightly horizontally striate on dorsal (outer) surface at base, finely papillose above, trabeculae weakly developed on both sides; endostome nearly as long as exostome, basal membranes low, segments filamentous, narrowly perforate, papillose, cilia rudimentary or absent. Spores lightly roughened, oblong to rounded-triangular, 34–64 µm long or round, 18–28 µm long. Calyptrae cucullate, densely hairy.

Pilotrichella is a genus of predominantly epiphytic, frequently pendulous mosses of tropical and subtropical American–African distribution. Brotherus (1906c) first positioned the genus (with sections *Orthostichella* and *Eupilotrichella*) in the tribe Meteorieae. This placement of *Pilotrichella* was followed by Fleischer (1908), who assigned the genus to the Meteoriaceae (tribe Pilotrichelleae). The association of *Pilotrichella* with the Meteoriaceae has been generally accepted (see, *e.g.*, Brotherus 1925; Bartram 1949; Florschütz 1964; Walther 1983; Vitt 1984; Spessard-Schueth 1994b; Churchill & Linares 1995; Duarte Bello 1997; Magill & Rooy 1998; Gradstein *et al.* 2001). The systematic placement of *Pilotrichella* was reconsidered by Buck (1994a, 1994b), who resurrected *Orthostichella* (as *Pseudopilotrichum* (Müll. Hal.) W. R. Buck & B. H. Allen) and transferred both genera, along with *Weymouthia* and *Squamidium*, to the Lembophyllaceae. In a revision of *Pilotrichella*, Allen and Magill (2003) also supported its placement in the Lembophyllaceae on the basis of its green, yellow-

ish red or brown, but never intensely black, coloration, enlarged alar cells, and ecostate leaves. Within the Lembophyllaceae, *Pilotrichella* appears isolated by virtue of its lack of a stem central strand, absolutely ecostate leaves, and more reduced peristome.

Pilotrichella is remarkably stable in most of its features. Its stolons, stems, and branches are morphologically identical, they lack a stem central strand, and its axillary hairs are usually reddish throughout. Interestingly, when the reddish coloration in the axillary hairs is weakly expressed it is the upper rather than the basal cells that remain colored. The stem and branch leaves of *Pilotrichella* are monomorphic, strongly concave, variously ovate in shape, and always lack a costa. Its leaf margins are generally broadly incurved and entire to serrulate, and its linear-flexuose leaf cells are often strongly porose. The alar cells in *Pilotrichella* are a distinctive feature of the genus. They are well developed and occur as excavate groups of reddish yellow, subquadrate to rectangular, porose cells.

The sporophytes of *Pilotrichella* are uniform throughout the genus. The setae are elongate and variously papillose-roughened. The genus has ovoid to short-cylindrical capsules, long-rostrate opercula, and hairy, cucullate calyptrae. The *Pilotrichella* peristome is diplolepideous and reduced, with yellowish white exostomes and endostomes that are nearly the same length. The more or less linear exostome teeth are lightly horizontally striate on the dorsal (outer) surface at base. The endostome has a low basal membrane with filamentous, narrowly perforate segments, and cilia are usually absent. Even though the peristome is significantly reduced, the presence at the base of the exostome teeth of horizontal striae seems to indicate the peristome is basically hypnoid.

Orthostichella differs significantly from *Pilotrichella* in its smaller plant size, and in often having primary stolons as well as stipitate stems. It also differs from *Pilotrichella* in having spirally ranked leaves with sparsely developed alar cells, and often its leaves have short double or single costae. Sporophytically the setae of *Orthostichella* are generally shorter than those of *Pilotrichella*. Additionally the presence of large spores (to 64 µm) in *Pilotrichella* is another feature that distinguishes the two taxa.

The name *Pilotrichella* combines the generic name *Pilotrichum* with the Latin substantival suffix *-ella* (diminutive).

1. Nearly all leaf apices erect, generally cuspidate to long-cuspidate; plants at times having slender branchlets with microphyllous leaves . . . . . 2. *P. mauiensis*
1. Most leaf apices reflexed, obtuse, broadly acute, mucronate, or apiculate; plants lacking slender branchlets 2

2. Plants lacking deciduous leaves. . . . . 1. *P. flexilis*
2. Plants with deciduous leaves . . . . . 1a. *P. flexilis* fo. *nudiramulosa*

1. *Pilotrichella flexilis* (Hedw.) Ångstr., Kongl. Svenska Vetensk. Acad. Handl. 33(11): 34. 1876. *Leskea flexilis* Sw. *ex* Hedw., Sp. Musc. Frond. 234. 1801. *Hypnum flexile* (Hedw.) Sw. *in* Brid., Muscol. Recent. 2(2): 153. 1801. *Hookeria flexilis* (Hedw.) Sm., Trans. Linn. Soc. London 9: 281. 1808. *Isothecium flexile* (Hedw.) Brid., Bryol. Univ. 2: 361. 1827. *Neckera flexilis* (Hedw.) Müll. Hal., Syn. Musc. Frond. 2: 129. 1850. *Meteorium flexile* (Hedw.) Mitt., J. Linn. Soc., Bot. 12: 438. 1869. *Pilotrichum flexile* (Hedw.) Müll. Hal. *in* Paris, Index. Bryol. (ed. 2) 4: 4. 1905. Protologue. Jamaica et insulae australes [*Swartz*]. Types (see Allen & Magill 2003). *Leskea flexilis* Spec. Musc. 234. Tab. 96. *Hypnum flexile* Swartz Prod. p. 141 (G, holotype); *Hypnum flexile* Swz. *N° 2069*, Herbarium Swartz (S, isotype); Jamaica, *Swartz* (H, isotype); a celeb D. D. Ol. Swartz. Jamaica (S, isotype); *Leskea flexilis* fl. ind. occ. from D. Swartz, Herb. Hooker, *H. 2592* (BM, isotype).

Pilotrichum cochlearifolium Müll. Hal., Linnaea 43: 599. 1843. *Neckera cochlearifolia* (Müll. Hal.) Müll. Hal., Syn. Musc. Frond. 2: 130. 1850. *Pilotrichella cochlearifolia* (Müll. Hal.) Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 223. 1872. *Meteorium cochlearifolium* (Müll. Hal.) Mitt. *ex* Paris, Index Bryol. (ed. 2) 4: 2. 1905. Protologue. Habitat in regno Mexicano, ubi legit Cl. *C. Ehrenberg*. Types (see Allen & Magill 2003). Mexico: leg. *C. Ehrenberg* (JE, lectotype); Mexico leg. *C. Ehrenberg* (H, S, isolectotypes).

Neckera turgescens Müll. Hal., Syn. Musc. Frond. 2: 131. 1850. *Meteorium turgescens* (Müll. Hal.) Mitt., J. Linn. Soc., Bot. 12: 440. 1869. *Pilotrichella turgescens* (Müll. Hal.) Besch., Mém. Soc. Sci. Nat. Cherbourg 16. 223. 1872. Protologue. Mexico: *C. Ehrenberg*. Types (see Allen & Magill 2003). Mexico. Er-

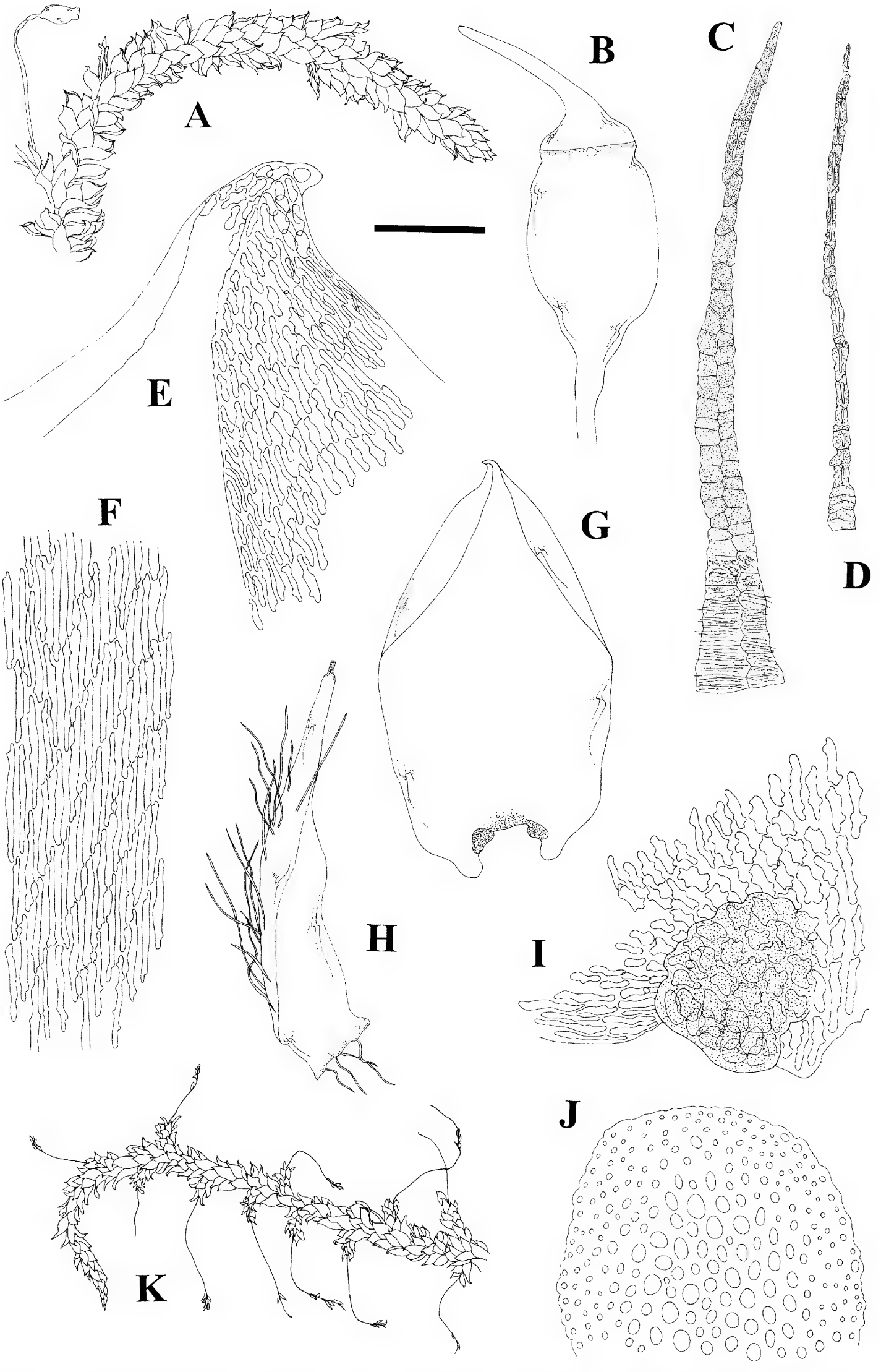
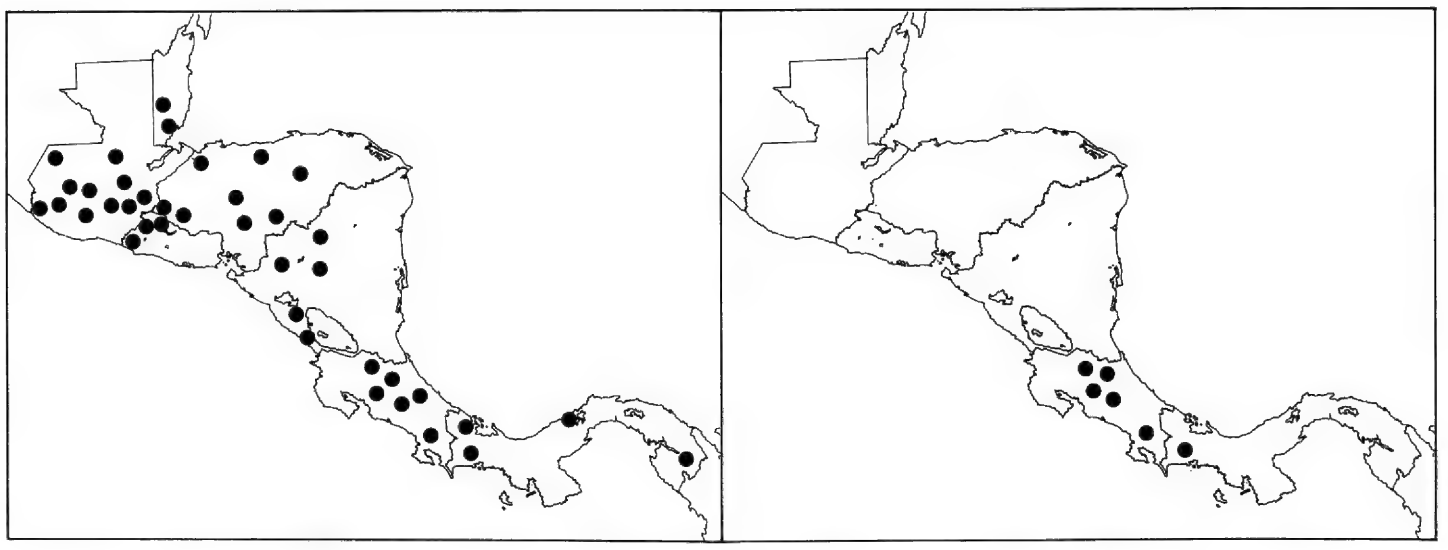


Figure 57. *Pilotrichella flexilis*. A. Habit. B. Seta, capsule, and operculum. C. Exostome, dorsal (outer) surface. D. Endostome, ventral (inner) surface. E. Leaf apex. F. Median leaf cells. G. Leaf. H. Calyptra. I. Alar cells. J. Stem in cross section. *Pilotrichella flexilis* fo. *nudiramosa*. K. Habit. Scale in mm: bar = 0.06 (E, F, I); bar = 0.08 (J); bar = 0.6 (G); bar = 0.9 (B, H); bar = 1.3 (C, D); bar = 6.4 (A, K). B, H from *Britton 100*; K from *Ule 867*; all other figure parts from *Allen 11549*.



Pilotrichella flexilis *Pilotrichella flexilis* fo. *nudiramulosa*

henberg. Muller in Hb. Hook. (BM, lectotype); Mexico. Erhenberg. Muller in Hb. Hook. (H, NY, isolectotypes); Mexico: *C. Ehrenberg* (S, isolectotype).

Meteorium orbifolium Mitt., J. Linn. Soc., Bot. 12: 440. 1869, illegitimate name, protologue includes an earlier name in synonymy. Based on: Mexico, *Ehrenberg* (H, JE, S); ins. Taboga [Panama], *Seemann*.

Pilotrichella recurvo-mucronata Müll. Hal., Bull. Herb. Boissier 5: 563. 1897. Protologue. Guadeloupe: *L'Herminier*: Puerto Rico, prope Uticado, in sylva primaeva: *Sintensis* 10. III. 1889. Types (see Allen & Magill 2003). Guadeloupe: *L'Herminier* (BM, lectotype); Guadeloupe: *L'Herminier* (H, FH, NY, S, isolectotypes).

Pilotrichella eroso-mucronata Müll. Hal., Bull. Herb. Boissier 5: 563. 1897. Protologue. Jamaica, New Haven Pass, inter *Capressinam arcuatipedem*: *W. Fawcett, 1896*. Type not seen, synonymized by Britton (1913).

Pilotrichella rigens Cardot, Rev. Bryol. 37: 8. 1910. Protologue. [Mexico] État de Hidalgo: Honey-station, 1904 (*Pringle, n. 15061*). Types (see Allen & Magill 2003). Plantae Mexicanae. State of Hidalgo, Honey Station, 10 May 1904, *C. G. Pringle 15061* (PC, holotype); Plantae Mexicanae. State of Hidalgo, Near Honey Station, 10 May 1904, *C. G. Pringle 15061* (NY, isotype).

Pilotrichella flexilis var. *robusta* Broth. *in* Thér., Mem. Soc. Cub. Hist. Nat. "Felipe Poey" 14: 360. 1940. Invalid name, no description given. Based on: Cuba, Sierra de Banao, Santa Clara (*Léon 8326*) (NY).

Pterobryopsis subcochlearifolia Thér. *in* H. A. Crum & Arzeni, Rev. Bryol. Lichénol. 22: 155. 1953. Invalid name, lacking a description and mentioned in synonymy. Based on: Panamá, s.l., *Bro Hélion*, 1906 (H).

Plants medium-sized to large, dull, light green, green, yellow green, reddish yellow, or golden brown, in loose mats, often with pendent strands. Primary stems yellow red, creeping, in cross section with sclerodermis of 4–6 small, thick-walled cells, cortical cells firm-walled, hyaline to yellow, central strand absent; rhizoids sparse, from circular clusters of initials abaxial to the leaf insertions, dark red, smooth to finely roughened, mostly not branched; paraphyllia absent; pseudoparaphyllia absent, scale leaves present; leaves reduced, erect to appressed, broadly ovate-oval, at times panduriform, 1.2–2.0 mm long, apex obtuse-rounded, mucronate to apiculate; cells linear-flexuose, thick-walled, porose; alar cells subquadrate to short-rectangular. Secondary stems horizontal, erect or pendent, to 30 cm long, irregularly branched; axillary hairs 3–5 cells long; basal cells 1–2, short, quadrate to subquadrate, upper cells 2–3, long-cylindrical, reddish throughout; rhizoids not seen. Secondary stem and branch buds short and swollen; leaves broadly oblong-ovate, not ranked, turgid, spreading to erect-spreading from the base, often with one margin broadly twisted inward when dry, erect to erect-spreading when wet, 1.7–3.0 × 1.6 mm, deeply concave, clasping at base, strongly to weakly auriculate; apices acute, generally mucronate, occasionally rounded or shortly apiculate, leaf tips mostly reflexed; margins broadly incurved above, often almost meeting at upper margins, entire below, variously serrulate directly below the apex; costa absent; cells linear-flexuose, median cells 50–80 × 4–6 µm, variously porose to occasionally smooth; basal cells shorter and broader, strongly and consistently porose; alar cells bulging in excavate groups, subquadrate to short-rectangular, 10–18 × 8–12 µm, usually dark red or reddish orange. Asexual reproduction at times by relatively short branches with deciduous leaves. Dioicous. Perigonia gemmate, lateral on secondary stems and branches, 1.0–1.5 mm long; perichaetia terminal on short lateral branches, unfertilized perichaetial leaves to 2 mm long.

Setae elongate, 3–15 mm long, smooth below and papillose above or papillose-roughened throughout, red. Capsules exserted, erect, ovoid to short-cylindrical, 1.8–2 mm long; exothecial cells subquadrate to irregularly short-rectangular, firm-walled; stomata superficial on neck; opercula long-rostrate, 1.6–2.0 mm long; annuli rudimentary; peristome yellowish white; exostome teeth 0.57 mm long, dorsal (outer) surface lightly horizontally striate at base, finely papillose above, trabeculae weakly developed on both sides; endostome nearly as long as exostome, basal membranes low, segments filamentous, narrowly perforate, papillose, cilia rudimentary or absent. Calyptrae cucullate, 3–6 mm long, densely hairy. Spores oblong, lightly roughened, 36–64 µm long.

Illustrations. Bartram (1949, Fig. 118 D–F); Potier de la Varde (1950, Fig. 5); Sharp *et al.* (1994, Fig. 536); Churchill and Linares (1995, Fig. 126 a–d); Buck (1998, Pl. 90 1–6); Duarte Bello (1997, Pl. 202); Parra Cuspoca *et al.* (1999, Fig. 42); Restrepo Restrepo and Para Cuspoca (2000, pp. 108–109); Gradstein *et al.* (2001, Fig. 156 L–O); Allen and Magill (2003, Figs. 3 & 4). Figure 57 A–J.

Habitat. Often pendent on tree trunks and branches, shrubs, palm fronds, vines, twigs, also on stumps, rotting logs, soil of road banks, boulders, and on ground; 600–3200 m.

Distribution in Central America. BELIZE. Cayo: *Allen 15238* (MO); Toledo: *Allen 18813* (BRH, MO). GUATEMALA. Alta Verapaz: *Standley 92407* (FH, NY); Chimaltenango: *Standley 58729* (FH); Chiquimula: *Steyermark 30601* (FH); El Progreso: *Steyermark 43550* (FH); Guatemala: *Standley 80694* (FH, NY); Huehuetenango: *Steyermark 48473* (FH, NY, US); Jalapa: *Steyermark 32487* (FH); Quetzaltenango: *Sharp 2207* (FH, MO, US); Sactepéquez: *Standley 65103* (FH); San Marcos: *Sharp 5472* (NY); Sololá: *Steyermark 47236* (FH, MO, NY); Totonicapán: *Standley 62651* (FH). EL SALVADOR. Ahuachapán: *Monro et al. 2051* (MO); Chalatenango: *Sipman 37656*(NY); Santa Ana: *Davidse et al. 37193* (MO). HONDURAS. Atlántida: *Allen 17364* (MO, TEFH); Comayagua: *Allen 13999* (MO, TEFH); Cortés: *Allen 14221* (MO, TEFH); El Paraíso: *Nelson 4799* (MO); Francisco Morazán: *Allen 12366* (MO, NY, TEFH); Lempira: *Allen 11273* (MO, TEFH); Ocotepeque: *Allen 14446* (MO, TEFH); Olancho: *Allen 12699* (MO, TEFH). NICARAGUA. Estelí: *Stevens 16296* (HNMN, MO, NY); Granada: *Almedo 1459a* (CINN, MO); Jinotega: *Henrich & Stevens 421* (HNMN, MO, NY); Matagalpa: *Davidse et al. 30505* (MO, S); Rivas: *Stevens 6543* (MO). COSTA RICA. Alajuela: *Croat 43482* (MO); Cartago: *King C91-80* (MO); Heredia: *Crosby 3879* (MO); Limón: *Davidse et al. 25797* (CR, MO); Puntarenas: *Lyon 147* (MO); San José: *Cryptogamae exsiccatae 3599* (B, BM, H, L, MO, NY, S, US). PANAMA. Bocas del Toro: *Allen 5236* (H, MO); Chiriquí: *Allen 5346* (MO); Colón: *Croat 33642B* (MO); Darién: *Allen 8896* (MO).

World range: Mexico; Central America; Caribbean; Western and Northern South America, Brazil); East Tropical Africa, Western Indian Ocean.

Pilotrichella flexilis is a common moss in Central America, where it grows in dense, pendent masses in shaded, very humid places. The species is remarkably stenotypic in most of its features and can often be recognized with a hand lens by its usually golden reddish color, turgid appearance, and erect-spreading leaves that are somewhat twisted above when dry and have consistently recurved mucros. Not all leaves in a single collection have recurved mucros, but the feature can always be found on at least some (usually most) leaves. The leaves near the branch buds are especially likely to have recurved mucros.

The leaves of *P. flexilis* are absolutely ecostate and consistently have auriculate leaf bases with bulging-excavate, generally dark red alar cells, linear-flexuose, strongly porose cells, and broadly incurved, usually serrulate upper margins. Although typically the leaves of *P. flexilis* are mucronate, mucro length varies considerably within the species. Plants at one end of the variation have many leaves with rounded apices and mucronate leaves occur only sporadically. At the opposite extreme there are plants with long-mucronate leaves that closely approach the leaves of *P. mauiensis*. This expression of *P. flexilis* differs from *P. mauiensis* in having distinctly recurved leaf mucros. The setae in *P. flexilis* are usually 10 mm long; however, their length can vary from 3–15 mm. This variation in seta length does not appear to have taxonomic value, since some collections have single stems with setae of length ranging from 3–11 mm.

Pilotrichella flexilis has been confused with *Squamidium nigricans* and *Phyllogonium viscosum*. These species are similar to *P. flexilis* in overall aspect, they grow in pendent masses, and their leaves have recurved mucros. *Squamidium nigricans* is a smaller plant than *P. flexilis*, it has spirally ranked

leaves, and often the plants have an intense blackish color. It also differs from *P. flexilis* in having immersed capsules, and leaves with long (but faint) single costae. The alar cells in *S. nigricans* are more extensively developed than those of *P. flexilis*, they are often hyaline rather than reddish yellow, and they are not as strongly bulging as the alar cells of *P. flexilis*. *Phyllogonium viscosum* and *P. flexilis* have auriculate leaves and linear-flexuose, strongly porose leaf cells. The genus *Phyllogonium* is characterized by its distichous, conduplicate leaves, and this feature usually can be relied on to separate it from *P. flexilis*. *Phyllogonium viscosum*, however, has swollen, turgid leaves that tend to obscure the distichous nature of the leaves. The costa in *Phyllogonium viscosum* varies from short-double to absent, and this feature can be used to distinguish it from *P. flexilis*, which is absolutely ecostate.

1a. *Pilotrichella flexilis* fo. ***nudiramulosa*** (Müll. Hal.) B. H. Allen & Magill, Egri Tanárképzö Föisk. Tud. Közlem. 24: 58. 2003. *Pilotrichella nudiramulosa* Müll. Hal., Hedwigia 40: 85. 1901. Protologue. Brasilia, S. Catharina, Serra Geral, ad truncos Araucariae Brasiliensis: *E. Ule*, Junio 1890, Coll. *No. 867*. Type (see Allen & Magill 2003). Brasilia, prov. S. Catharina, Serra Geral, an Stammen von Araucaria, Junii 1890. leg. *E. Ule 867* (H, lectotype).

Illustrations. Allen and Magill (2003, Fig. 2 F). Figure 57 K.

Habitat. On tree trunks and branches; 800–2700 m.

Distribution in Central America. COSTA RICA. Alajuela: *Brenes 16691* (FH, NY); Cartago: *Standley 33582* (FH, US); Heredia: *Tonduz s.n.* [Pl. Costaricensis *N^o^ 5680*] (G); Puntarenas: *Haber 6211* (CR, MO, NY); San José: *Crosby 10882* (CR, MO). PANAMA. Chiriquí: *Croat 13746* (MO).

World range: Mexico; Central America; Western South America, Brazil; Western Indian Ocean.

Plants of *Pilotrichella flexilis* fo. *nudiramulosa* are generally smaller than those of *P. flexilis*, and they usually have short branches with leaves so deciduous that the branches are often naked. The form, however, exhibits considerable gametophytic variation throughout its range, especially in the development of deciduous leaves. *Pilotrichella mauiensis* is similar in size to forma *nudiramulosa*, and sometimes it also has short branches with deciduous leaves. The presence of flagelliform branch tips in *P. mauiensis*, as well as slender branchlets with microphyllous leaves, will often distinguish it from *P. flexilis* fo. *nudiramulosa*. Furthermore, the leaves of *P. mauiensis* are not nearly as auriculate at base as those of *P. flexilis*, and its usually cuspidate leaf apices are erect rather than recurved.

2. *Pilotrichella mauiensis* (Sull.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 255. 1877. *Meteorium mauiensis* Sull., Proc. Amer. Acad. Arts 3: 182. 1855. Protologue. [Hawaii] East Maui, Sandwich Islands; on the north bank of the Crater, at an elevation of 10,200 feet. Types (see Allen & Magill 2003). East Maui, Sandwich Islands; on the north bank of the crater Haleakala, U.S.E.E. Wilkes 1838/42 (FH, holotype). East Maui–north Bauky [sic] Crater, 10,200 ft. high! Sandwich Island, Herbarium of the U. S. Exploring Expedition under the Command of Capt. Wilkes (NY, isotype); East Maui, Wilkes Expl. Exp. (NY, isotype); East Maui–North Bank of Crater–10,200 ft. alt. Sandwich Isds. U. S. Ex. Ex. (NY, isotype); Hawaii, Wilkes Exped. E. Maui (FH, isotype).

Pilotrichella flagellifera Besch., Mexic. Pl. 39. 1872, illegitimate name, protologue includes an earlier name in synonymy. Based on: Mejico (*Ehrenberg*); Orizaba (*Bourgeau*), (both at BM).

Pilotrichella cochlearifolia var. *flagellifera* Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 223. 1872. Protologue. [Mexico] Orizaba (*Bourgeau*). Type (see Allen & Magill 2003). Mexico, Orizaba, 1866: *Bourgeau*, Herb. Émil Bescherelle: 1900 (BM, lectotype).

Meteorium vulcanicum Mitt. *in* Seem., Fl. Vit. 395. 1873. Protologue. Hawaii ad montem ignivomen (Macrae! in Herb. Musaei Brit.).Type (see Allen & Magill 2003). Owyhee. ad m. ignivomen. Macrae, Jan. 1825, *sin. coll.* (FH, isotype).

Pilotrichella desmoclada Müll. Hal., Flora 82: 464. 1896. *Weymouthia desmoclada* (Müll. Hal.) Broth., Nat. Pflanzenfam. I(3): 812. 1906. Protologue. Insulae Hawaiicae, sine loco speciali, sed vero-similiter e regionibus altioribus: *Dr. Hildebrand*. Types (see Allen & Magill 2003). Hawaii: sine loco designato. leg. *Dr. Hildebrand* (H, lectotype); Hawaii: sine loc spec., leg. *Dr. W. Hildebrand* (FH, isolectotype); Hawaii. leg. *Hildebrand* (H, isolectotype).

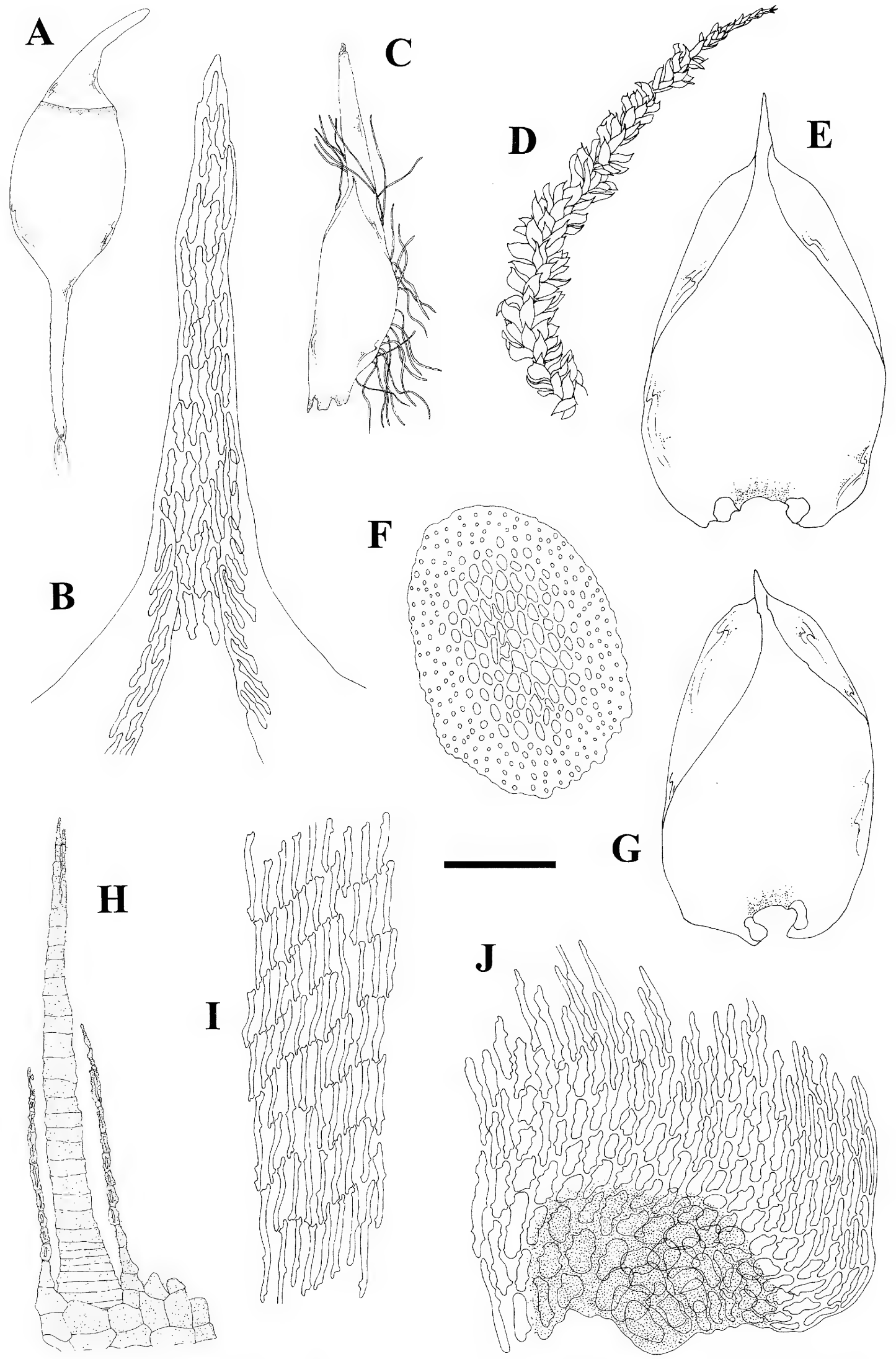
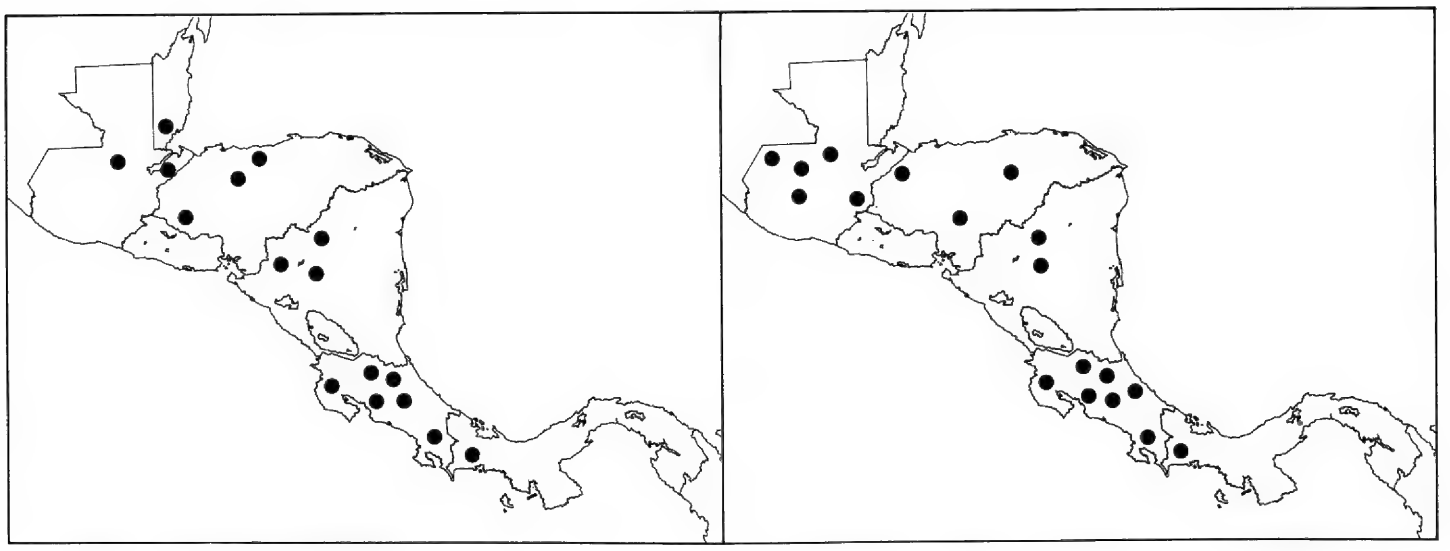


Figure 58. *Pilotrichella mauiensis*. A. Seta, capsule, and operculum. B. Leaf apex. C. Calyptra. D. Habit. E & G. Branch leaves. F. Stem in cross section. H. Endostome, ventral (inner) surface. I. Median leaf cells. J. Basal and alar cells. Scale in mm: bar = 0.06 (B, I, J); bar = 0.08 (F); bar = 0.13 (A, C, H); bar = 0.5 (E, G); bar = 3.2 (D). B, E, J from *Allen 17364*; D, I from *Hoe 3548*; F from the type; all other figure parts from *Pringle 10417*.



Pilotrichella mauiensis *Calyptothecium duplicatum*

Plants medium-sized, dull, light green, yellow green, or golden brown, in stiff mats, sometimes with pendent strands. Primary stems yellow red to red, creeping; stems in cross section with sclerodermis of 4–6 rows of thick-walled cells, cortical cells firm-walled, hyaline to yellow, central strand absent; rhizoids from circular clusters of initials abaxial to the leaf insertions, dark red, smooth to finely roughened, mostly not branched; paraphyllia absent; pseudoparaphyllia absent, scale leaves present; leaves reduced, erect-clasping, broadly ovate, auriculate at base, 0.8–1.0 mm long, acuminate, hair-pointed; upper margins serrulate; cells linear-flexuose, thick-walled, strongly porose; alar cells dark red, subquadrate to short-rectangular. Secondary stems arising irregularly from the primary stems, creeping or pendent, to 25 cm long, irregularly branched; axillary hairs 4–5 cells long; cells reddish, basal cells 1–2, short, quadrate to subquadrate, upper cells 2–3, long-cylindrical; rhizoids present. Secondary stem and branch apices short and swollen; leaves broadly ovate to oblong-ovate, not ranked, wide-spreading to erect-spreading from the base with margins incurved when dry, erect-spreading when wet, 1–2 mm long, concave, clasping at base, rounded to the insertion or weakly auriculate, acuminate, long- or short-cuspidate, leaf tips straight not reflexed; margins broadly incurved above, entire below, serrulate directly below the apex; costa absent; leaf cells linear-flexuose, porose throughout, median cells 16–50 × 3–4 μm; basal cells shorter and broader; alar cells in bulging, excavate groups, subquadrate to short-rectangular, 14–20 × 2–12 μm, yellow red, reddish orange, or red. Asexual reproduction often by slender branches with microphyllous leaves, flagelliform branch tips, or deciduous leaves. Dioicous. Perigonia gemmate, lateral on secondary stems and branches, 1.0–1.3 mm long; perichaetia terminal on short lateral branches, unfertilized perichaetial leaves to 2.5 mm long. Setae elongate, 5–15 mm long, red, smooth to lightly roughened below, papillose above. Capsules exserted, erect, ovoid to short-cylindrical, 1.5–2.0 mm long; exothecial cells subquadrate to irregularly subrectangular, firm-walled; stomata superficial on neck; opercula long-rostrate, 1.0–1.5 mm long; annuli rudimentary; peristome yellowish white, exostome to 0.5 mm long, dorsal (outer) surface lightly horizontally striate at base, finely papillose above, trabeculae weakly developed on both sides; endostome nearly as long as the exostome, basal membranes low, segments filamentous, narrowly perforate, papillose, cilia rudimentary or absent. Calyptrae cucullate, hairy, to 3.5 mm long. Spores round, irregularly rounded to oblong, lightly roughened, 20–28 μm long.

Illustrations. Bartram (1933a, Fig. 125); Allen and Magill (2003, Figs. 5–7). Figure 58.

Habitat. On tree trunks, pendent from branches, on shrubs, vines, or twigs; 120–3109 m.

Distribution in Central America. BELIZE. Toledo: *Allen 18831* (BRH, MO). GUATEMALA. Alta Verapaz: *Standley 90725* (FH); Zacapa: *Steyermark 43227* (FH). HONDURAS. Atlántida: *Allen 17399A* (MO); Lempira: *Allen 11596* (MO); Yoro: *Allen 13589* (MO). NICARAGUA. Estelí: *Stevens & Grijalva 15632* (HNMN, MO); Jinotega: *Henrich & Stevens 283* (MO); Matagalpa: *Granow de la Cerda 2167* (MO, NY). COSTA RICA. Alajuela: *Brenes 16985* (NY); Cartago: *Standley 41487* (FH, JE, S, US); Guanacaste: *Dodge et al. 7915* (FH); Heredia: *Crosby 10870* (H, NY); Puntarenas: *Croat 47131* (MO); San José: *Stevens 13704* (MO). PANAMA. Chiriquí: *Croat 16057* (MO, S).

World range: North-Central Pacific; Mexico; Central America; Caribbean; Western South America.

Pilotrichella mauiensis was described from the Hawaiian Islands, where it exhibits considerable variation in plant size and overall aspect. Even so, the variations exhibited by Hawaiian plants do not demonstrate the full range of variation found in the species. For example, plants of *P. mauiensis* from southern Mexico, Guatemala, Belize, and northern Honduras can be especially large and have long-cuspidate leaves (see, *e.g.*, *Hermann 28836*, NY or *Allen 17364*, MO). When first encountered, this extreme Neotropical expression seems distinct from the Hawaiian *P. mauiensis*, but throughout its range there is complete intergradation in plant size and leaf cuspid length. Leaf cuspid length is also remarkably variable within single collections. Critical features that separate *P. mauiensis* from other members of *Pilotrichella* include its erect, usually cuspidate leaf apices, weakly auriculate leaf bases, alar cells differentiated in a relatively small, discrete area, the occurrence of flagelliform-attenuate branch apices, and the presence of slender branchlets with microphyllous leaves.

Although the slender branchlets in this species appear axillary, they arise on the dorsal side of the leaf from the line of cells that marks the transition from the alar region to the laminal cells. Since each originates from a single cell, they are extremely deciduous. When young the branchlets have the same appearance as axillary propagula in *Pohlia*, and as they begin to elongate they look similar to the axillary brood branches of *Pseudotaxiphyllum elegans* (Brid.) Z. Iwats. When fully formed they can be 15 mm long and have microphyllous leaves with axillary brood bodies. These branchlets also occur around branch primordia. Newton (2002) gave an excellent, detailed account of these branchlets. Although Newton (2002) attributed these structures to *P. flexilis*, flagelliform branchlets are unknown in that species and her plants almost certainly are *P. mauiensis*.

The leaves of *P. flexilis* and *P. mauiensis* are similar in the form and distribution of their alar cells, and in both the leaves are sometimes deciduous. Plants of *P. flexilis* are generally larger than those of *P. mauiensis*, and their leaf apices are more consistently mucronate, with most of the apices distinctly recurved. *Pilotrichella flexilis* also never has flagelliform branch apices or slender branchlets.

PTEROBRYACEAE

Pterobryaceae Kindb., Gen. Eur. N.-Amer. Bryin. 15. 1897.

Plants slender, medium-sized, or robust in loose or dense mats, at times pendent, or frondose. Primary stems creeping, with erect to imbricate, distantly spaced leaves; secondary stems irregularly spaced, erect or pendent, stipitate or not stipitate, pinnately to bipinnately branched or not to occasionally branched, branches at times becoming flagellate, or transformed into stoloniferous stems; stems in cross section with sclerodermis, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous; rhizoids red brown, roughened or papillose, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions, and leaves on attenuate branch tips, and at base of stipes. Secondary stem leaves spirally ranked or not, erect-spreading, imbricate, wide-spreading, squarrose, or complanate, smooth, lightly undulate, rugose, or plicate, acute or acuminate, concave or plane, rounded to the insertion, cordate or auriculate, variously decurrent; margins entire, serrulate, papillose-serrulate, or denticulate, plane or revolute; costae double or single, rarely absent; cells linear to linear-flexuose, variously porose, smooth, pro, uni- or pluripapillose, firm-walled, cells across the insertion yellowish, porose; alar cells weakly or strongly developed. Asexual reproduction by hyaline, smooth, uniseriate, septate gemmae arising from large, circular clusters of initials in leaf axils or deciduous branch leaves. Dioicous (rarely autoicous). Setae short or long, smooth, lightly papillose, or scabrose. Capsules immersed or exserted, erect, symmetric, cylindric, short-cylindric, ovoid, or spherical; stomata absent; opercula conic-rostate; annuli rudimentary; peristome diplolepideous, exostome irregularly developed, weakly trabeculate, often with a well-developed prostome; endostome rudimentary or absent. Calyptra cucullate or mitrate, smooth or sparsely hairy.

The Pterobryaceae are a tropical family of 25 genera (Buck & Goffinet 2000; Goffinet & Buck 2004). Many of its genera have only a few species, and generic boundaries within the family are often weakly defined. The Pterobryaceae are frequently medium-sized to large plants with creeping primary stems and erect (sometimes pendent), irregularly spaced, at times stipitate, secondary stems. The secondary stems can be pinnately or bipinnately branched. Allen (1987f) found distinctive filamentous pseudoparaphyllia in all members of the family. Other consistent features of the family include stems without central strands, capsules that lack stomata, rudimentary annuli, and irregularly formed peristomes with well-developed prostomes but greatly reduced endostomes.

Leaves within the Pterobryaceae are often differentiated into four kinds (primary stem, stipe, secondary stem, and branch), and they are sometimes clearly arranged in spiral rows. The leaf cells are typically elongate-flexuose, firm-walled, and porose. Alar cells are often well developed. Most members of the Pterobryaceae are dioicous, and sporophytes are not common within the family. Pterobryaceae capsules are erect, but capsule shape is extremely variable, and the setae can be long or short. In some large genera some species have immersed capsules, while others have exserted capsules. The spores are often large in size. The calyptrae are typically cucullate; however, mitrate calyptrae also occur, and sometimes both types can be found in the same genus. Many members of the family reproduce asexually by hyaline, uniseriate, septate gemmae that arise from large, circular clusters of initials in leaf axils or from deciduous branch leaves.

Arzeni (1954) treated the family in Central America and the West Indies, while Argent (1973a, b) revised the African species of Pterobryaceae. Magill (1983) provided a circumscription of the family, and he surveyed the odd peristome types found in the Pterobryaceae.

1. Leaves with costae absent or faintly short and double 2
1. Leaves with at least some leaves having single costae reaching to midleaf 4

2. Leaves (especially when wet) in distinct spiral rows . . . . . 4. *Orthostichidium*
2. Leaves evenly foliate 3

3. Stems not or rarely branched; leaves wide-spreading to squarrose; axillary, uniseriate, asexual gemmae often present . . . . . 3. *Jaegerina*
3. Stems irregularly pinnately branched; leaves erect to imbricate; asexual gemmae absent . . . . . 9. *Renauldia*

4. Plants irregularly branched, not stipitate, pendent; secondary stem and branch leaves strongly spirally ranked . . . . . 5. *Orthostichopsis*
4. Plants not branched or irregularly pinnately branched, at times stipitate, frondose or dendroid, rarely pendent; leaves not or weakly spirally branched 5

5. Leaves plicate 6
5. Leaves smooth or undulate 7

6. Plants not stipitate, not or sparsely branched; leaf margins revolute nearly throughout; cells papillose; alar cells well developed . . . . . 2. *Henicodium*
6. Plants stipitate, frondose, and regularly pinnately branched; leaf margins plane; cells smooth; alar cells not or weakly developed . . . . . 7. *Pterobryon*

7. Leaves more or less complanate, cordate-auriculate at base . . . . . 1. *Calyptothecium*
7. Leaves evenly foliate, turgid, erect-spreading or squarrose, rounded at the base 8

8. Alar cells consisting of 15–30 rows of subquadrate cells 9
8. Alar cells consisting of a few subquadrate cells at basal angles 10

9. Leaf margins revolute nearly throughout; cells unipapillose . . . . . 2. *Henicodium*
9. Leaf margins plane; cells smooth . . . . . 8. *Pterobryopsis*

10. Plants stipitate, typically frondose, or pinnately branched; leaves erect to spreading . . . . . 6. *Pireella*
10. Plants not stipitate, not or rarely branched; leaves wide-spreading to squarrose . . . . . 3. *Jaegerina*

1. *Calyptothecium* Mitt., J. Linn. Soc., Bot. 10: 190. 1868. *Pterobryon* Hornsch. sect. *Calyptothecium* (Mitt.) Mitt., J. Linn. Soc., Bot. 12: 427. 1869. *Pterobryon* Hornsch. subgen. *Calyptothecium* (Mitt.) Mitt., Trans. Roy. Soc. Victoria 19: 81. 1882.

Pterobryopsis M. Fleisch. sect. *Pseudo-Calyptothecium* Broth., Nat. Pflanzenfam. I(3): 802. 1906. *Calyptothecium* sect. *Pseudo-Calyptothecium* (Broth.) Wijk & Margad., Taxon 8: 72. 1959.
Calyptothecium sect. *Pseudo-Neckera* Broth., Nat. Pflanzenfam. I(3): 839. 1906, illegitimate name, includes type of the genus.
Calyptothecium sect. *Pseudo-Pterobryopsis* M. Fleisch., Musci Buitenzorg 3: 859. 1908, illegitimate name, nomenclaturally superfluous.
Orthorrhynchidium Renauld & Cardot, Suppl. Prodr. Fl. Bryol. Madagascar. 71. 1909.

Plants medium-sized to robust in loose or dense mats, at times pendent. Primary stems creeping with erect to imbricate distantly spaced leaves; secondary stems irregularly spaced, erect or pendent, stipitate, irregularly pinnately branched or not to occasionally branched, branches often becoming flagellate, or transformed to stoloniferous stems; stems in cross section with sclerodermis, cortical cells enlarged, firm- to thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous; rhizoids red brown, roughened or papillose, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions, on leaves of attenuate branch tips, and at base of stipes. Secondary stem complanate-foliate, leaves spreading, oblong-ovate or ovate-lanceolate, smooth, lightly undulate or rugose, gradually acute, concave, rounded to the insertion or cordate-auriculate, not decurrent; margins entire throughout or lightly serrulate at the apex, plane; costae variable, when short and faint either single or double, when slender and reaching midleaf single; cells linear to linear-flexuose, smooth or porose, firm-walled; alar cells weakly developed. Asexual reproduction by hyaline, smooth, uniseriate, septate gemmae arising from large, circular clusters of initials in leaf axils. Dioicous (monoicous in Africa). Setae short or long, smooth or lightly papillose. Capsules immersed or exserted, erect, symmetric, cylindric, short-cylindric, or ovoid; stomata absent; opercula conic-rostate; annuli rudimentary; peristome diplolepideous; exostome teeth yellow, narrowly triangular, smooth to finely roughened, weakly trabeculate, often with a well-developed prostome; endostome present or absent. Spores round, lightly papillose. Calyptrae cucullate, smooth or sparsely hairy.

Calyptothecium is a genus of 29 species (Crosby *et al.* 2000), most of which occur in Asia. Plants of *Calyptothecium* are fairly large, often pinnately branched and characteristically have complanate leaves that are frequently auriculate and have weakly developed alar cells. In many of its features *Calyptothecium* is extremely variable. There are some species of *Calyptothecium* that have leaves only rounded to the insertion, and many species have turgid-forms that are not at all complanate. The costa can be absent, short and double, or variously single. The capsules of *Calyptothecium* can be immersed or exserted, cylindrical or ovoid, and the endostome of its diplolepideous peristome can be present or absent. Most species of *Calyptothecium* have pinnately branched stems, but there is one, *C. planifrons*, in which the stems are mostly unbranched. Renauld and Cardot (Renauld 1909) established the genus *Orthorrhynchidium* for this species. They also considered it to differ from *Calyptothecium* in having non-porose leaf cells, but at times the leaf cells in *C. planifrons* are weakly porose. As noted by Buck (1998) *Calyptothecium* seems to be a weak segregate of *Jaegerina*. Indeed, when considered on a worldwide basis it differs from *Jaegerina* only in having complanate or variously flattened leaves. The African species of *Calyptothecium* were revised by Argent (1973a).

The name *Calyptothecium* combines the Greek *calypt* (covered or a cover) with the Greek *thekion* (a small vessel), and this apparently refers to its immersed capsules.

1. Plants 4–40 cm tall; stems densely branched; leaves rugose; apices plane; median leaf cells 5–6 µm wide; capsules immersed . . . . . 1. *C. duplicatum*
1. Plants to 4.5 cm tall; stems rarely branched; leaves plane or lightly undulate; apices galeate; median leaf cells 2–4 µm wide; capsules exserted . . . . . 2. *C. planifrons*

1. *Calyptothecium duplicatum* (Schwägr.) Broth., Nat. Pflanzenfam. I(3): 839. 1906. *Hypnum duplicatum* Schwägr., Sp. Musc. Frond. Suppl. 1(2): 198. 1816. *Pterobryon duplicatum* (Schwägr.) Mitt., J. Linn. Soc., Bot. 12: 427. 1869. *Neckera duplicata* (Schwägr.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 279. 1877. Protologue. Sterile in insula Dominica lectum habeo.

Neckera acutifolia Brid., Bryol. Univ. 2: 757. 1827. *Calyptothecium acutifolium* (Brid.) Broth. *in* Paris, Index Bryol. (ed. 2) 1: 288. 1904. *Pterobryopsis acutifolium* (Brid.) Magill, Fl. S. Africa, Bryophyta I(3): 569. 1998. Protologue. [Réunion] In insulâ Bourbonis habitat. Clar. Desvaux sterile communicavit. Type. Réunion. N° XI. *N. Distichia acutifolia. Pterogonium.* an ins. borbonia (B, holotype), *syn. nov.*

Fissidens dominicensis Brid., Bryol. Univ. 2: 707. 1827, illegitimate name, includes an earlier name in synonymy. Based on: In insulâ Dominicâ habitat. Quis detexerit nos latet. Fructus non visus.

Schistophyllum dominicense Brid., Bryol. Univ. 2: 707. 1827, illegitimate name, included in synonymy.

Neckera porodictyon Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 29(1): 180. 1890. *Calyptothecium porodictyon* (Renauld & Cardot) Broth., Nat. Pflanzenfam. I(3): 839. 1906. Protologue. Haïti, Port au Price, ad truncos arborum (*Bertrand*).

Calyptothecium turgescens Broth. & Thér. *in* Thér., Recueil Publ. Soc. Havraise Études Diverses 88: 312. 1921. Protologue. [Costa Rica] La Palma, près San José, alt. 1500 m (*C. Werklé*, avril 1910). Types. Costa Rica. La Palma, 1500 m, leg. *C. Werkle*, comm. Brotherus (FH, isotype); Costa Rica, San José, alt. 1500 meter, *Chas. Werklé*, April 1900 (FH, isotype).

Plants medium-sized to robust, in green to yellow green, loose or dense mats, often pendent. Primary stems creeping with erect to imbricate distantly spaced leaves; secondary stems irregularly spaced, erect or pendent, stipitate, irregularly pinnately branched, branches often becoming flagellate, or transformed to stoloniferous stems, stipe leaves evenly foliate, 4–40 cm long; stems in cross section with sclerodermis of 4–7 rows of small, reddish yellow, thick-walled cells, cortical cells enlarged, yellowish to hyaline, firm- to thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous; rhizoids red brown, roughened, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions, on leaves of attenuate branch tips, and at base of stipes. Secondary stem variously complanate-foliate, leaves spreading, 2.5–3.5 mm long, oblong-ovate, rugose, gradually acute, concave, cordate-auriculate to subauriculate at base, not decurrent; margins entire throughout or lightly serrulate at the apex, plane; costae variable: either short, faint, and single or double, or slender, reaching midleaf, and single; cells linear to linear-flexuose, porose and firm-walled throughout, apical cells 40–60 × 6–8 µm, median cells 50–85 × 5–6 µm; basal cells 40–90 × 6 µm; alar cells weakly developed, rhombic to short-rectangular in 2–5 rows.

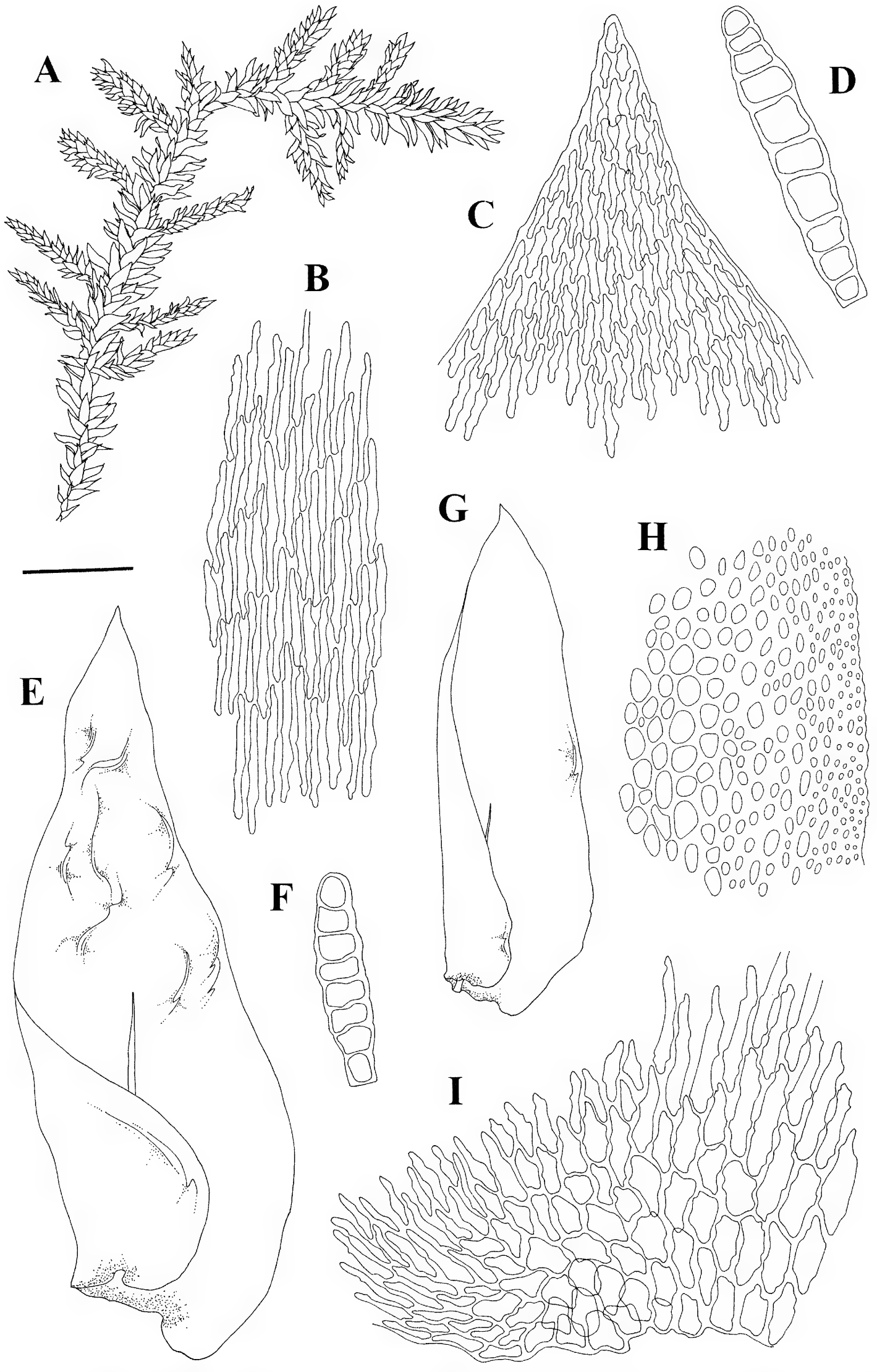


Figure 59. *Calyptothecium duplicatum*. A. Habit. B. Median leaf cells. C. Leaf apex. D & F. Gemmae. E. Stem leaf. G. Branch leaf. H. Stem in cross section. I. Basal and alar cells. Scale in mm: bar = 0.06 (B–D, F, I); bar = 0.08 (H); bar = 0.5 (E, G); bar = 5.1 (A). All figure parts from *Allen 12801*.

Branches weakly complanate-foliate to turgid; leaves imbricate, oblong-ovate to oblong-lanceolate, 2.0–2.5 mm long, rounded to cordate at base, otherwise similar to stem leaves. Asexual reproduction by hyaline, smooth, uniseriate, septate gemmae arising from large, circular clusters of initials in leaf axils. Dioicous. Sporophytes not seen, description from Buck (1998) and Wagner (1951). Setae short, smooth, to 0.85 mm long. Capsules erect, symmetric, short-cylindric to ovoid, to 2 mm long; exothecial cells short-rectangular, firm-walled; opercula conic-rostrate; annuli rudimentary; peristome diplolepideous; exostome teeth yellow, narrowly triangular, smooth to finely roughened, weakly trabeculate, often with a well-developed prostome; endostome not seen. Spores round, lightly papillose, to 21 μm.

Illustrations. Thériot (1921, Fig. 5); Bartram (1949, Fig. 123 F–G, Fig. 124 A–B); Wagner (1951, Pl. 19); Sharp *et al.* (1994, Fig. 535); Churchill and Linares (1995, Fig. 165 a–b); Duarte Bello (1997, Pl. 182); Buck (1998, Pl. 57); Gradstein *et al.* (2001, Fig. 194 A–B). Figure 59.

Habitat. On tree branches and trunks, often pendent, on vines, rotting logs, rocks, or boulders, and on ground amongst soil and litter; 500–3200 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: *Sharp 2977* (FH, US); Chimaltenango: *Godman & Salvin* (NY); Chiquimula: *Steyermark 31710* (F, FH, NY); Huehuetenango: *Sharp 5009* (F, FH, MO, US); Quiché: *Sharp 2419* (FH). HONDURAS. Francisco Morazán: *Richards et al. 3512* (F, MO, NY); Olancho: *Allen 12801* (MO, TEFH); Santa Bárbara: *Crosby 2794* (MO). NICARAGUA. Jinotega: *Henrich & Stevens 421B* (MO); Matagalpa: *D'Arcy* (F, MO). COSTA RICA. Alajuela: *Brenes* (NY); Cartago: *Standley & Valerio 49485* (FH, US); Guanacaste: *Crosby 3847* (MO); Heredia: *Crosby 10862* (BM, CR, DUKE, F, FH, G, H, MO, NY, US); Limón: *Alfaro* (F); Puntarenas: *Lyon 123* (CR, MO); San José: *Griffin & Morales B103* (F, MO, NY). PANAMA. Canal Area: *Dodge 3982* (NY); Chiriquí: *Cornman 3190* (F, FH, MO, US).

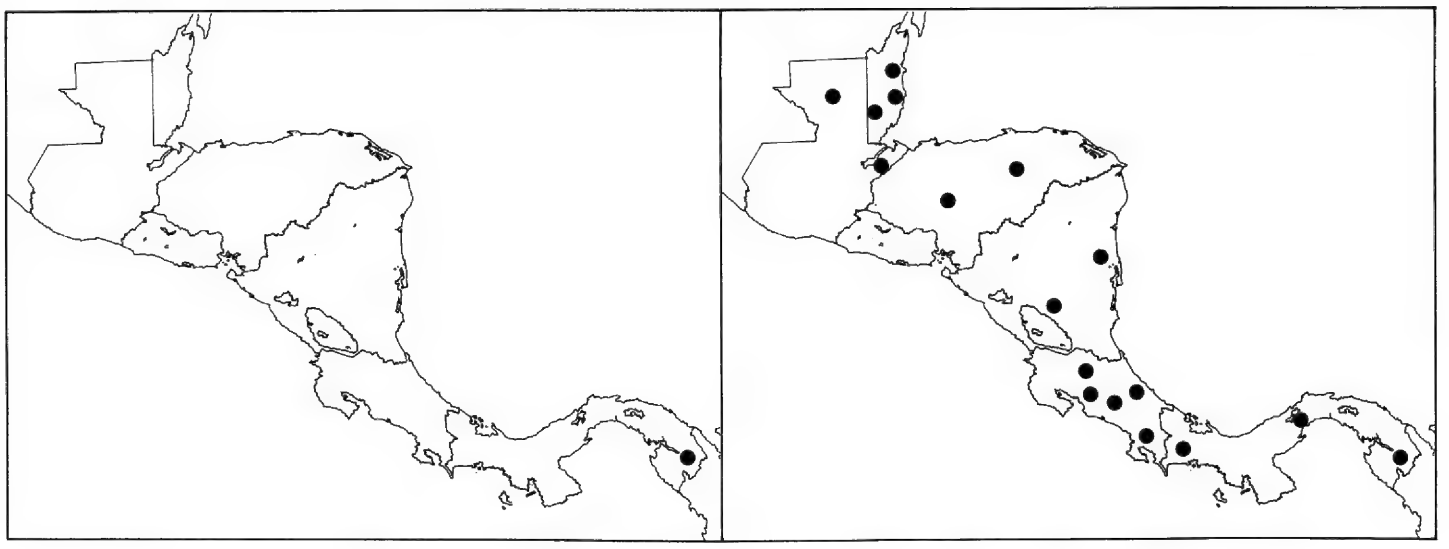
World range: Mexico; Central America; Caribbean; Western and Northern South America; Brazil; West, West-Central, East, and South Tropical Africa, Southern Africa, Western Indian Ocean.

Calyptothecium duplicatum is a medium-sized to robust species commonly found on trees in wet forests at elevations above 1000 meters. The species occasionally occurs on rocks or soil. Plants of *C. duplicatum* are typically densely branched and have variably complanate, gradually acute, rugose leaves. There is, however, a form with turgid, non-complanate leaves found throughout the range of the species. This form also has leaves that are strongly auriculate at base and have fairly well-developed alar cells. It is especially common in Costa Rica, where it was described as *C. turgescens.* The *turgescens*-form at times appears quite distinct, but there are many collections intermediate in form between it and typical *C. duplicatum*. The leaf costae in *C. duplicatum* are typically single and reach midleaf. However, the feature is remarkably variable, and leaves with forked or double costae can often be found along with single-costate leaves.

Plants of *Calyptothecium planifrons* are usually much less tall than those of *C. duplicatum* (3.0–4.5 cm vs. 4–40 cm), and its stems are not or only occasionally branched. Furthermore, the leaves of *C. planifrons* are not or hardly undulate and their apices are distinctly galeate. The median leaf cells of *C. planifrons* are also narrower than those of *C. duplicatum* (2–4 μm vs. 5–6 μm). Although the capsules in *C. planifron*s are exserted while those of *C. duplicatum* are immersed, this distinction is not very useful since sporophytes are rare in both species.

Phyllogonium viscosum is a pendent species similar in size to *Calyptothecium duplicatum*. In addition, the leaves in both species are turgidly complanate, undulate, and auriculate at base. *Phyllogonium viscosum* differs from *C. duplicatum* in having truly distichous leaves, cucullate leaf apices, consistently short and double or absent costae, and foliose pseudoparaphyllia. There are some Central American species of *Neckera* similar to *C. duplicatum* in leaf stance and form as well as having filamentous pseudoparaphyllia. However, their plants are smaller and more slender than those of *C. duplicatum*, their leaves have consistently short, double costae, and they commonly are found with sporophytes.

Buck (1998) called attention to the similarity of the African *C. acutifolium* (Brid.) Broth. to *C. duplicatum*; he suspected they might be synonymous. In this regard it is interesting to note that *C. acutifolium* has turgid-forms very similar to the *turgescens*-form of *C. duplicatum*. The turgid-forms of *C. acutifolium* have been recognized (Argent 1973a) at the varietal level. I can find no differences between *C. acutifolium* and *C. duplicatum* and consider the two synonymous.



Calyptothecium planifrons *Henicodium geniculatum*

2. *Calyptothecium planifrons* (Renauld & Paris) Argent, J. Bryol. 7: 565. 1973. *Garovaglia planifrons* Renauld & Paris, Rev. Bryol. 29: 7. 1902. *Orthorrhynchidium planifrons* (Renauld & Paris) Renauld & Cardot, Suppl. Prodr. Fl. Bryol. Madagascar 72. 1909. Protologue. Madagascar. Antoagazi, *s. coll. & no.*

Plants medium-sized, in green to yellow green, loose or dense mats. Primary stems creeping with erect to imbricate, distantly spaced, minute scale leaves. Secondary stems irregularly spaced, erect, shortly stipitate, not or occasionally branched, at times becoming flagellate, or transformed to stoloniferous stems, 1.0–4.5 cm long; stems in cross section with sclerodermis of 4–7 rows of small, red, very thick-walled cells, cortical cells enlarged, yellow, thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous; rhizoids red brown, roughened to papillose, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions, and at base of stipes. Stipes evenly foliate. Secondary stems variously complanate-foliate, leaves spreading, 2.0–2.5 mm long, ovate-lanceolate, smooth or lightly undulate, concave, galeate above, narrowly acute, apex often reflexed, rounded to the insertion, not decurrent; margins entire throughout or lightly serrulate at the apex, plane; costae variable, short, faint and either single or double, slender and reaching above midleaf; cells linear to linear-flexuose, not or weakly porose, firm-walled, 50–90 × 2–4 µm; cells across the insertion reddish orange, porose, rectangular; alar cells weakly developed, rhombic to short-rectangular in 2–4 rows. Asexual reproduction by hyaline, smooth, uniseriate, septate gemmae arising from large, circular clusters of initials in leaf axils. Dioicous. Setae 5 mm long, lightly papillose, red or yellowish. Capsules erect, symmetric, cylindric, to 2.0–2.7 mm long; exothecial cells at mouth red, quadrate, firm-walled, in 5–7 rows, lower exothecial cells rectangular, thin-walled; stomata absent; operculum not seen; annulus not seen; peristome diplolepideous; exostome teeth yellow, narrowly triangular, smooth to finely roughened, weakly trabeculate, prostome present; endostome not seen. Spores round, lightly papillose, to 24–38 µm. Immature calyptrae lightly roughened, sparsely hairy.

Illustrations. Renauld (1909, Pl. 16 fig. 2); Argent (1973a, Fig. 1); Churchill and Linares (1995, Fig. 165 c–e); Gradstein *et al.* (2001, Fig. 194 C–D). Figure 60.

Habitat. On tree trunks and treelet branches; 800–900 m.

Distribution in Central America. PANAMA. Darién: *Allen 8952* (MO).

World range: Central America; Western and Northern South America; Brazil; Northeast, West-Central, East, and South Tropical Africa, Western Indian Ocean.

Calyptothecium planifrons is an African species first reported in the Neotropics by Reese (1985) from Brazil. It is also present in Colombia (*Churchill et al. 14780*, MO) and Suriname (*Allen 25512*, MO, NY). Plants of *C. planifrons* are generally smaller than those of *C. duplicatum*, and the secondary stems are not or only occasionally branched. It further differs from *C. duplicatum* in having leaves

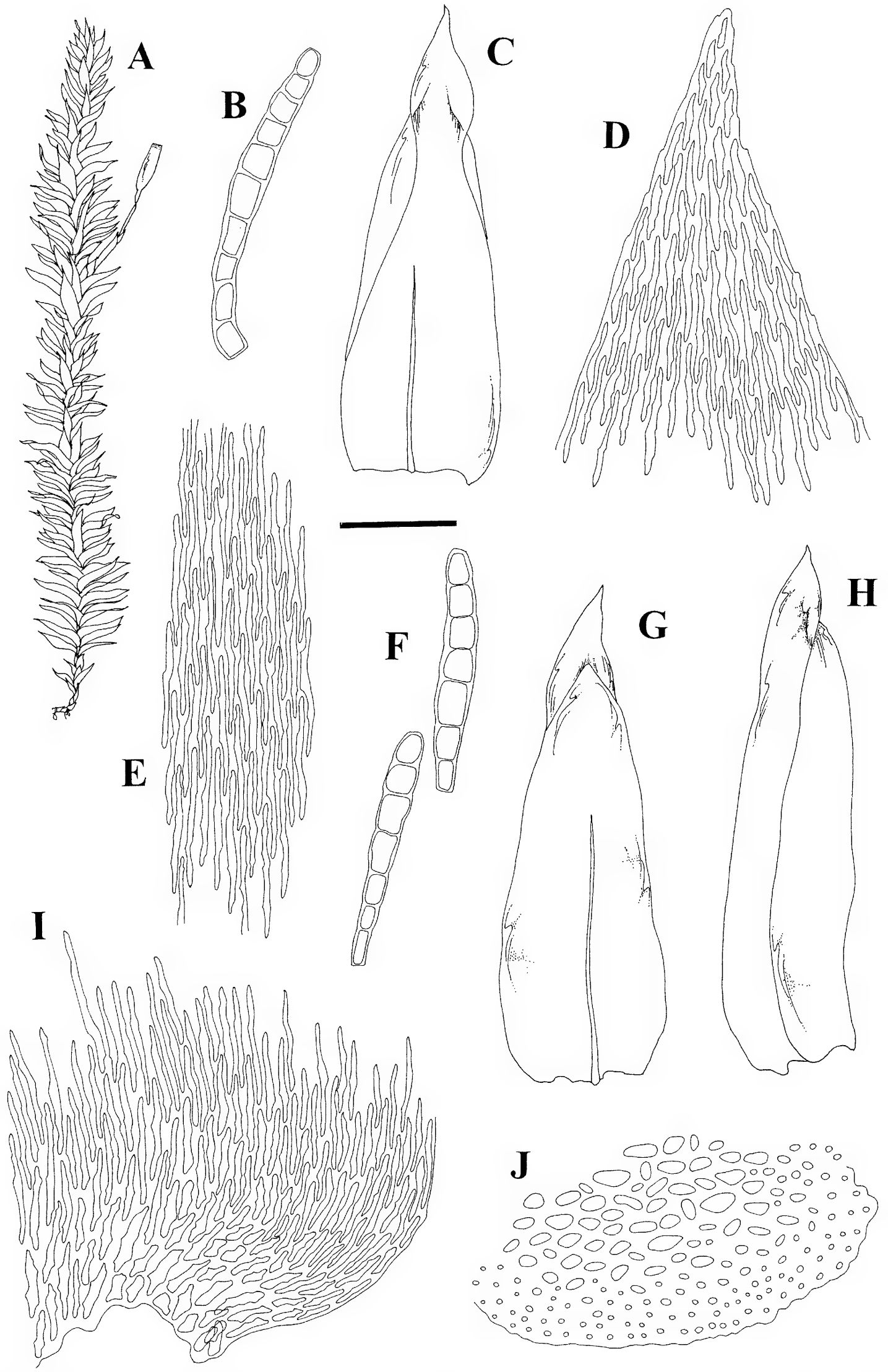


Figure 60. *Calyptothecium planifrons*. A. Habit. B & F. Gemmae. C, G & H. Leaves. D. Leaf apex. E. Median leaf cells. I. Basal and alar cells. J. Stem in cross section. Scale in mm: bar = 0.06 (B, D–F, I, J); bar = 0.5 (C, G, H); bar = 5.1 (A). All figure parts from *Allen 8977*.

that are distinctly galeate above, rounded rather than cordate-auriculate to the insertion, and much narrower leaf cells. Two of the three Panamanian collections of *C. planifrons* examined have both spear-stage and old sporophytes. These collections indicate the species has a pterobryaceous peristome (*i.e.*, irregularly developed diplolepideous, with the endostome apparently lacking, and properistome present); however, the capsules were too old for a comprehensive study of their sporophytic features. The setae of *C. planifrons* have been described as smooth (Argent 1973a), but the setae on the Panamanian collections are lightly roughened-papillose.

Argent (1973a) described the secondary stems of *C. planifrons* as ". . . at first erect, becoming pendent." Plants of *C. planifrons* from Panama and Suriname, however, have secondary stems that grow horizontally rather than pendent from tree trunks. Strongly complanate plants of *C. planifrons* can be confused in the field with robust collections of *Catagonium*; it differs from *Calyptothecium planifrons* in having leaves with short and double or absent costae. As noted by Argent (1973a), plants of *C. planifrons* are sometimes weakly complanate with mostly concave rather than conduplicate leaves. This expression of the species parallels the turgid-form of *C. duplicatum* and can be confused in the field with *Jaegerina scariosa*, which differs from *C. planifrons* in having broadly ovate, erect-patent to squarrose leaves, with thicker-walled cells.

2. *Henicodium* (Müll. Hal.) Kindb., Enum. Bryin. Exot. 16. 1888. *Hypnum* sect. *Henicodium* Müll. Hal., Linnaea 39: 470. 1875.

Leucodontopsis Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32(1): 177. 1893 ["*Leucodoniopsis*"].

Plants slender to medium-sized, green to yellow green, in loose or dense mats. Primary stems creeping, with erect to imbricate, distantly spaced, small leaves; rhizoids red brown, roughened-papillose, irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions and at base of secondary stems. Secondary stems irregularly spaced, erect, not stipitate, not or occasionally branched, often becoming flagellate; stems in cross section with sclerodermis, enlarged cortical cells, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous; leaves appressed to erect-spreading when dry, spreading when wet, not ranked, lanceolate, oblong-lanceolate, or oblong-ovate, plicate, concave, broadly acuminate, rounded to the insertion, decurrent; margins papillose-serrulate, typically revolute throughout; costae single, slender and reaching 2/3 the leaf length; stems in cross section with cells more or less homogeneously thickened, ventral cells somewhat enlarged; upper and median cells linear to linear-flexuose, with 1–4 papillae, not or weakly porose, firm-walled; cells across the insertions yellowish, porose, rectangular; alar cells well developed, subrectangular, quadrate, or oblate, collenchymatous. Asexual reproduction by smooth, hyaline, uniseriate, septate gemmae arising from large, circular clusters of initials in leaf axils. Dioicous. Setae elongate. Capsules erect, symmetric, short-cylindric to ovoid-cylindric; operculum and annulus unknown; peristome diplolepideous; exostome teeth pale yellow, narrowly triangular, more or less smooth, prostome present; endostome smooth, segments keeled, perforate, almost as long as the exostome, basal membranes low. Spores spherical, finely papillose. Calyptra not seen.

Henicodium has long been known in Central America as *Leucodontopsis*, a genus traditionally placed in the Leucodontaceae (Brotherus 1925; Bartram 1949; Florschütz 1964; Crum & Anderson 1981; Walther 1983; Vitt 1984). Buck (1989) synonymized *Henicodium* (an older name) and *Leucodontopsis*. Akiyama (1988) first suggested the transfer of *Henicodium* (as *Leucodontopsis*) to the Pterobryaceae because it had filamentous pseudoparaphyllia. Buck (1989) transferred the genus to the Pterobryaceae on the basis of its creeping, more or less naked primary stems, filamentous pseudoparaphyllia, single costate leaves with relatively short, papillose leaf cells (the papillae over the lumina), numerous alar cells, and exostomial prostome.

Crosby *et al.* (2000) considered *Henicodium* monospecific; however, there are three names in the genus *Leucodontopsis* (*L. geniculata*, *L. siamensis* Dixon, and *L. cameruniae* (Broth.) Broth.), and only the type of *L. geniculata* has been examined. Tan and Mohamed (1990) tentatively synonymized *L. siamensis* with *H. geniculatum* on the basis of recently collected material. On the basis of examined, non-type material, Dixon (1935) and Buck (1989) thought the genus was probably monospecific.

Henicodium has mostly unbranched secondary stems that often have axillary gemmae. The leaves are plicate and usually stiffly erect when dry. Microscopically the leaves are distinctive in having

strongly revolute margins, long, single costae, uni- to pluripapillose leaf cells, and very well-developed, quadrate to oblate, thick-walled alar cells.

The derivation of the name *Henicodium* is uncertain. Müller gave no direct indication of the meaning of the name. Furthermore, the Greek components of the name, *henos* (old, former) and *kodia* (head), are not very informative. The name, however, is in some way connected to the name *Oticodium*, which was used by Müller (1875) at the same time for a different section of *Hypnum*.

Henicodium geniculatum (Mitt.) W. R. Buck, Bryologist 92: 534. 1989. *Leucodon geniculatus* Mitt., J. Linn. Soc., Bot. 12: 409. 1869. *Leucodontopsis geniculata* (Mitt.) H. A. Crum & Steere, Sci. Surv. Porto Rico & Virgin Islands 7(4): 511. 1957. Protologue. Ins. Jamaica, *Wilds*. Fl. Amazon, Tauaú prope Pará, ramicola, *Spruce, n. 1515*. Andes Peruvianae, in monte Guayrapurina, *Spruce*. Brasilia, Rio de Janerio, *Milne*.

Hypnum niam-niamiae Müll. Hal., Linnaea 39: 468. 1875. *Henicodium niam-niamiae* (Müll. Hal.) Kindb., Enum. Bryin. Exot. 16. 1888. *Leucodontopsis niam-niamiae* (Müll. Hal.) Broth., Nat. Pflanzenfam. I(3): 1214. 1919 ["*Leucodoniopsis niam-niamiae*"]. Protologue. [Sudan/Zaire] Niam-niam-regiones, Nuporruporru, in fissura terrae inter *Schwetschleam Schweinfurthi*, 1. Martio 1871. [*Schweinfurth*]. Type (see Buck 1989). Niam-niam, Nuporruporru, 1 Mar. 1871, *Schweinfurth s.n.* (NY, lectotype).

Neckera floridana Austin, Bot. Gaz. (Crawfordsville) 4: 152. 1879. *Pilotrichella floridana* (Austin) Kindb., Enum. Bryin. Exot. 28. 1888. *Leucodontopsis floridana* (Austin) E. Britton, Bryologist 15: 28. 1912. Protologue. On trees, Caloosa, Florida, March 1878, *J. D. S* [*mith*]. and *C. F. A* [*ustin*].

Leucodontopsis plicata Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32(1): 177. 1893 ["*Leucodoniopsis plicata*"]. Protologue. [Costa Rica] Boruca (*Pitt.* [*ier*], *N^o^ 5616*).

Plants slender to medium-sized, green to yellow green, in loose or dense mats. Primary stems creeping with erect to imbricate, distantly spaced, small leaves; rhizoids red brown, roughened-papillose, irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions and at base of secondary stems. Secondary stems irregularly spaced, erect, not stipitate, not or occasionally branched, often becoming flagellate, 1.0–3.5 cm long; stems in cross section with sclerodermis of 3–4 rows of small, red, very thick-walled cells, cortical cells enlarged, yellow, thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous; leaves appressed to erect-spreading when dry, spreading when wet, not ranked, lanceolate, oblong-lanceolate, or oblong-ovate, 1–2 mm long, plicate, concave, broadly acuminate, rounded to the insertion, decurrent; margins papillose-serrulate, typically revolute throughout; costae single, slender and reaching 2/3 the leaf length; in cross section cells more or less homogeneously thickened, but ventral cells somewhat enlarged; upper and median cells linear to linear-flexuose, with 1–4 papillae, not or weakly porose, firm-walled, 30–60 × 3–4 µm; cells across the insertion yellowish, porose, rectangular; alar cells well developed, subrectangular, quadrate, or oblate, collenchymatous, in 20–40 rows. Asexual reproduction by smooth, hyaline, uniseriate, septate gemmae arising from large, circular clusters of initials in leaf axils. Dioicous. Sporophytes not seen, description from Florschütz (1954) and Buck (1998). Setae elongate, 4–6 mm long, smooth, orange. Capsules erect, symmetric, short-cylindric to ovoid-cylindric, 1.7–2.0 mm long; exothecial cells oblate at mouth, lower exothecial cells hexagonal, firm-walled; operculum and annulus not seen; peristome diplolepideous; exostome teeth pale yellow, narrowly triangular, more or less smooth, prostome present; endostome smooth, segments keeled, perforate, almost as long as the exostome, basal membranes low. Spores spherical, finely papillose, 25–33 µm. Calyptra not seen.

Illustrations. Britton (1912, Figs. 1–4); Bartram (1949, Fig. 110 F–H); Florschütz (1954, Fig. 5); Breen (1963, Pl. 110 7–10); Florschütz (1964, Fig. 96); Crum and Anderson (1981, Fig. 366); Reese (1984, Fig. 43 H–J); Tan and Mohamed (1990, Fig. 2); Churchill (1994, Fig. 34 B); Sharp *et al.* (1994, Fig. 502); Churchill and Linares (1995, Fig. 165 f–i); Duarte Bello (1997, Pl. 176); Buck (1998, Pl. 60 1–7); Gradstein *et al.* (2001, Fig. 194 E–H); Buck (2003, Fig. 111). Figure 61.

Habitat. On bark of tree trunks and branches, fallen branches, or rotting wood, collected once on an iron rail; 10–1600 m.

Distribution in Central America. BELIZE. Belize: *Allen 17966* (MO); Cayo: *Bartlett 13094* (FH, NY); Stann Creek: *Schipp S114* (F, FH). GUATEMALA. Izabal: *Kellerman 7590b* (US); Petén: *Lun-*

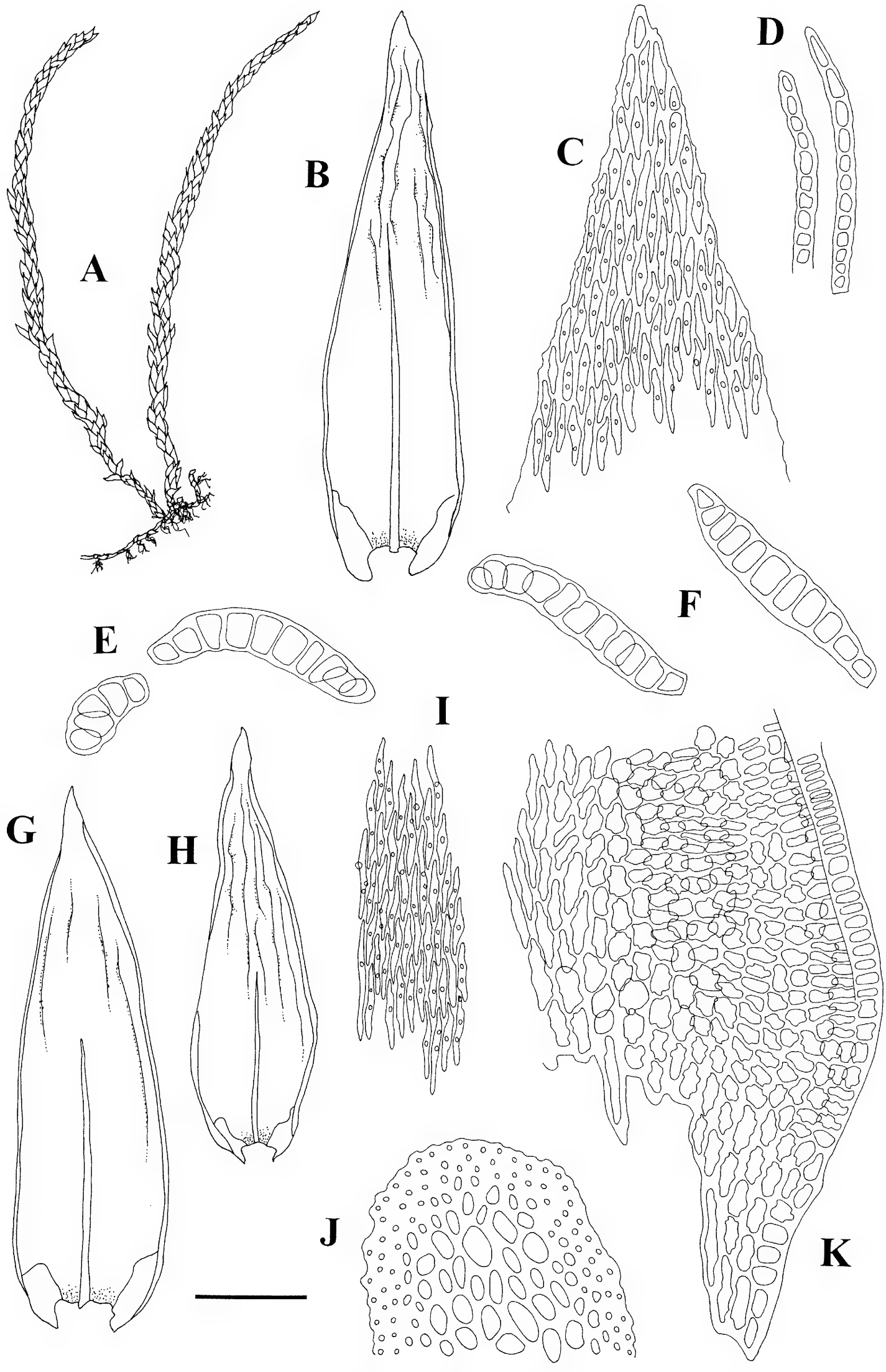


Figure 61. *Henicodium geniculatum*. A. Habit. B, G & H. Leaves. C. Leaf apex. D. Pseudoparaphyllia. E & F. Gemmae. I. Median leaf cells. J. Stem in cross section. K. Basal and alar cells. Scale in mm: bar = 0.06 (C–F, I–K); bar = 0.4 (B, G, H); bar = 4.3 (A). All figure parts from *Allen 13406*.

dell 2220 (F, FH, US). HONDURAS. Comayagua: *Allen 13406* (MO); Olancho: *Allen 12912* (MO). NICARAGUA. Chontales: *Stevens 2862A* (MO); Zelaya: *Stevens 12661D* (MO). COSTA RICA. Alajuela: *Alfaro 174* (FH, US); Cartago: *Holm & Iltis 1228* (FH, MO); Limón: *Alfaro s.n.* (FH, US); Puntarenas: *Hammel 18271* (MO); San José: *Alfaro 90a* (F, FH). PANAMA. Canal Area: *Willis 50* (F, FH, MO, US); Chiriquí: *Cornman 3006A* (MO); Darién: *Allen 9019B* (MO).

World range: Southeastern U.S.A.; Mexico; Central America; Caribbean; Western and Northern South America, Brazil; West, Northeast and West-Central Tropical Africa; Malesia.

Henicodium geniculatum is a slender to medium-sized species with usually erect, unbranched, secondary stems. It typically has stout, oblong-lanceolate or oblong-ovate leaves that are erect-appressed when dry, but occasional plants have slender, lanceolate leaves that are erect-spreading when dry. Thériot (1925) established varieties (var. *latifolia* and var. *gracilis*) for these two distinctive forms of *H. geniculatum*. Florschütz (1954) found that leaves of both varieties can occur on the same plant and that leaves intermediate in form can also be found. Thériot (1925) described *H. geniculatum* as an autoicous species and figured cross-striae on the dorsal surface of its exostome. This indicated to Buck (1998) that Thériot had examined a mixed collection, and indeed Florschütz (1954) found that the sporophyte in the collection Thériot examined belonged to *Sematophyllum subpinnatum*.

Henicodium geniculatum has leaf margins that are usually recurved throughout, and Buck (1998) reported and figured the leaf cells as unipapillose. In Central America some plants of *H. geniculatum* have only unipapillose leaf cells, but more often plants have a mixture of uni- and pluripapillose leaf cells. Florschütz (1964, Suriname plants), Crum and Anderson (1981, Florida plants), and Duarte Bello (1997, Cuban plants) figure the leaf cells of *H. geniculatum* as both uni- and pluripapillose. Other distinctive features of *H. geniculatum* include its long, single costae, exceptionally well-developed, quadrate to oblate alar cells, common presence of uniseriate gemmae in the leaf axils, irregularly branched rhizoids, and the tendency of its secondary stems to become long attenuate with broad, appressed leaves.

Henicodium geniculatum is often confused with *Pseudocryphaea domingensis*. That species, however, is more regularly branched, and its leaves are smoothly imbricate, with percurrent costae and smooth leaf cells. Furthermore, *P. domingensis* lacks axillary gemmae but usually has numerous flagellate branches.

3. *Jaegerina* Müll. Hal., Linnaea 40: 273. 1876 ["*Jägerina*"].

Jaegerinopsis Broth., Nat. Pflanzenfam. I(3): 790. 1906.

Plants small, medium-sized, or robust in lax tufts or loose mats on trees. Primary stems creeping with small, erect to imbricate, distantly spaced leaves; rhizoids red brown, smooth to roughened, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions and at base of secondary stems. Secondary stems irregularly spaced, erect, not stipitate, not or rarely branched; stems in cross section with sclerodermis, enlarged, firm- to thick-walled cortical cells, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous; stem tips at times becoming flagellate; leaves spreading, wide-spreading, or squarrose, gradually lanceolate, broadly ovate, or ovate-lanceolate, acute or acuminate, concave, cordate at base, not or very shortly decurrent; margins entire to serrulate, plane; costae short and double or single; upper and median cells linear-flexuose, smooth or prorate, variably porose, firm-walled throughout; alar cells weakly developed, cells across the insertions yellow. Asexual reproduction by smooth, hyaline, uniseriate, septate gemmae arising from large, circular clusters of initials in leaf axils, germinating from both ends, new filaments coarsely papillose. Dioicous. Perichaetial leaves sheathing the lower part of the setae. Setae elongate, smooth to lightly roughened below. Capsules erect, symmetric, elliptic to short-cylindric; exothecial cells at mouth red, quadrate to oblate, thick-walled in several rows, lower exothecial cells short-rectangular, firm-walled; stomata absent; opercula conic-rostrate; annuli rudimentary, of firm-walled cells; peristome diplolepideous; exostome teeth pale yellow to hyaline, rudimentary, smooth or finely roughened, weakly trabeculate, prostome present; endostome absent. Calyptrae cucullate, naked or lightly hairy.

Jaegerina is a genus of nine species (Crosby *et al.* 2000) mostly found in Africa, especially the Mascarene Islands. The genus is epiphytic, with distinct, stoloniferous primary stems and erect, irregularly spaced, mostly unbranched secondary stems. The leaves are generally spreading to squarrose, and often clasping. The leaf costae in *Jaegerina* are extremely variable, and sometimes single stems can have leaves with costae single, short and double, or absent. The upper and median leaf cells in *Jaegerina* are elongate to linear, usually thick-walled, porose, and at times prorate. The alar cells are weakly differentiated. *Jaegerina* can have immersed or exserted capsules that vary from cylindrical to almost spherical, apiculate or rostrate opercula, and calyptrae varying from hairy-mitrate to smooth-cucullate. Variation in the sporophytes and calyptrae of *Jaegerina* appears to be taxonomically important, but, as noted by Argent (1973a), sporophytes in the group are rare or unknown. *Jaegerinopsis* was separated from *Jaegerina* on the basis of a cucullate rather than mitrate calyptra and broad, short-acuminate leaves rather than lanceolate, acuminate leaves. Argent (1973a) found no obvious discontinuity between the leaves of *Jaegerina* and *Jaegerinopsis*, and because of the impracticality of the calyptral feature synonymized them, as did Buck (1998).

Although *Jaegerina* has not been the subject of a worldwide revision, many of the species have been treated within regional accounts. Hyvönen (1989) treated the only South Asian species of *Jaegerina*. Argent (1973a) revised the mainland Africa species of *Jaegerina*, and he gave a key to the African and Madagascan species of the genus. Arzeni (1954) accounted for the genus in the southern United States, Mexico, Central America, and the West Indies. Buck (1998) more recently treated the genus in the Caribbean.

The name *Jaegerina* is given in honor of the German apothecary and bryologist August Jäger (2 July 1842–23 August 1877). Jäger was born and died in Freiburg im Breisgau, but is often erroneously considered a Swiss bryologist (see Frahm & Eggers 2001). He is the primary author of *Genera et Species Muscorum systematice disposita seu Adumbriatio florae muscorum totius orbis terrarium*, which was originally published in the Swiss journal Bericht über die Thätigkeit der St. Gallischen Naturwissenschaftlichen Gesellschaft. His herbarum is now at NY.

1. Leaves lanceolate, long-acuminate; costae subpercurrent; margins serrate throughout; some or all upper leaf cells prorate . . . . . 1. *J. guatemalensis*

1. Leaves broadly ovate to ovate-lanceolate, acute to broadly acuminate; costae short and double or single and ending just above midleaf; margins serrulate to entire; upper leaf cells smooth . . . . . 2. *J. scariosa*

1. *Jaegerina guatemalensis* E. B. Bartram, Bryologist 49: 116. 1946. Protologue. Guatemala. Dept. Izabal: between Bananera and "La Prensa" in Montaña del Mico, alt. 50–100 m, *Steyermark 38205, 39202 type*; northeast of San Felipe, alt. 50–100 m, *Steyermark 39648*. Types. Guatemala. Dept. Izabal: between Bananera and "La Prensa" in Montaña del Mico, alt. 50–150 m, April 9 1940 *Steyermark 39202* (FH, holotype; F, isotype). Guatemala. Dept. Izabal: between Bananera and "La Prensa" in Montaña del Mico, alt. 50–100 m, *Steyermark 38205* (F, FH, paratypes); Dept. Izabal: jungle bordering Quebrada Roseúl, lower slopes bordering eastern part of Cerro Santa Cruz, northeast of San Felipe, alt. 50–150 m, April 18 1940, *Steyermark 39648* (F, FH, MO, NY, paratypes).

Jaegerina jamaicensis E. Britton *ex* Broth., Nat. Pflanzenfam. (ed. 2) 11: 139. 1925, invalid name, lacks a description. Based on: Jamaica Hills near Troy, Jan. 1910, *J. King Brown 11173, 11183* (FH, NY).

Plants medium-sized to robust, in green to yellow green, glossy, lax tufts or loose mats on trees. Primary stems creeping with small, erect to imbricate, distantly spaced leaves; rhizoids red brown, smooth to roughened, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions and at base of secondary stems. Secondary stems irregularly spaced, erect, not stipitate, not or rarely branched, 3–6 cm long; stems in cross section with sclerodermis of 3–5 rows of small, reddish yellow, thick-walled cells, cortical cells enlarged, yellowish to hyaline, firm- to thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous; leaves spreading, wide-spreading, or squarrose, 3.0–5.5 mm long, gradually lanceolate from an ovate base, gradually long-acuminate, concave, cordate at base, not or very shortly decurrent; margins serrulate throughout,

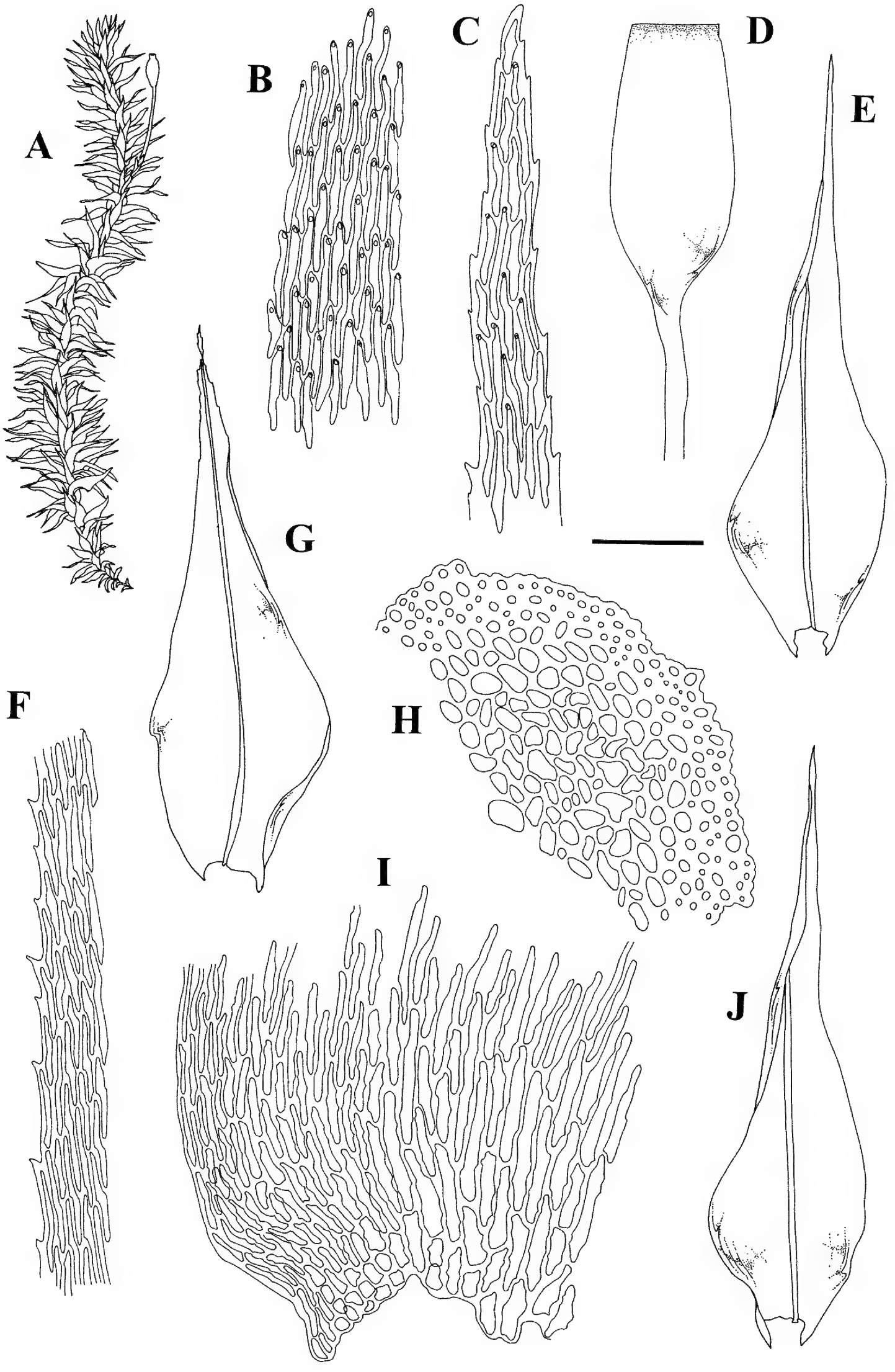
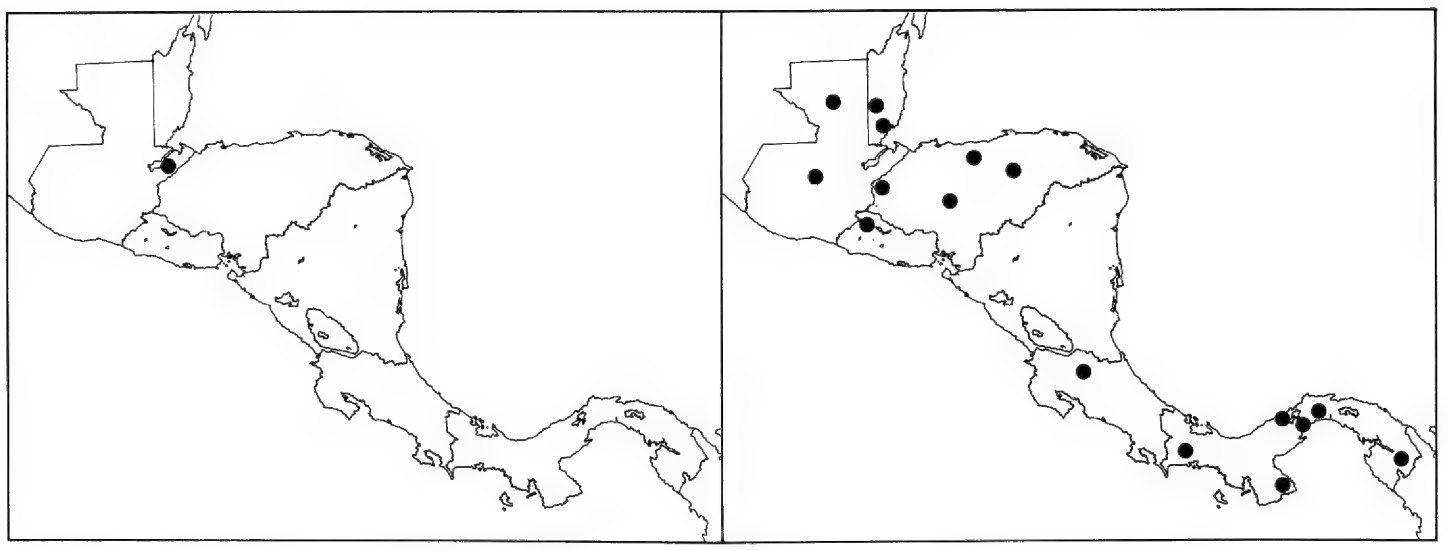


Figure 62. *Jaegerina guatemalensis*. A. Habit. B. Median leaf cells. C. Leaf apex. D. Seta and capsule. E, G & J. Leaves. F. Median leaf cells and margin. H. Stem in cross section. I. Basal and alar cells. Scale in mm: bar = 0.06 (B, C, F, H, I); bar = 0.7 (E, G, J); bar = 0.9 (D); bar = 5.1 (A). A, D from *Steyermark 39202*; all other figure parts from *Steyermark 39648*.



Jaegerina guatemalensis *Jaegerina scariosa*

plane; costae single, slender, subpercurrent; cells linear-flexuose, smooth or prorate, variably porose, firm-walled throughout, apical cells 28–38 × 5–15 µm, median cells 40–70 × 5–8 µm; alar cells weakly developed, of a few irregularly subquadrate, incrassate cells at the basal angles, cells across the insertions yellow. Asexual reproduction by smooth, hyaline, uniseriate, septate gemmae arising from large, circular clusters of initials in leaf axils, germinating from both ends, new filaments coarsely papillose. Dioicous. Perichaetial leaves sheathing the lower 1/4 of the setae, 3–4 mm long. Setae smooth, reddish brown, 5–8 mm long. Capsules erect, symmetric, elliptic to short-cylindric, 1.8–2.3 mm long; exothecial cells at mouth red, quadrate to oblate, thick-walled, in 6–8 rows, lower cells short-rectangular, firm-walled; stomata absent; opercula conic-rostrate, 1.0–1.5 mm long; annuli rudimentary, of firm-walled cells; peristome diplolepideous; exostome teeth pale yellow to hyaline, rudimentary, truncate-triangular, to 225 µm long, finely roughened, weakly trabeculate, prostome present; endostome absent. Spores round, smooth to lightly papillose, 14–16 µm. Immature calyptrae 2.5–3.0 mm long, lightly hairy.

Illustrations. Bartram (1949, Fig. 112 D–F); Arzeni (1954, Pl. 2 1 & Pl. 3); Buck (1998, Pl. 56 10–17). Figure 62.

Habitat. On bark of trees; 50–100 m.

Distribution in Central America. GUATEMALA. Izabal: *Steyermark 39648* (F, FH, MO, NY).

World range: Central America; Caribbean.

Jaegerina guatemalensis is a robust species with erect, unbranched, or rarely branched, secondary stems. It has wide-spreading to squarrose, lanceolate leaves that are cordate at base, with single, subpercurrent costae, prorate upper leaf cells, and very weakly developed alar cells. *Jaegerina scariosa* is smaller than *J. guatemalensis* in all respects. It further differs from *J. guatemalensis* in having ovate to broadly ovate-lanceolate leaves with acute to broadly acuminate apices, entire to serrulate margins, and smooth cells. The costa in *J. scariosa* can be short and double or single, but if single it reaches only to about midleaf.

In Central America *J. guatemalensis* is presently known from only three Guatemalan collections, all in the northeastern Department of Izabal. It is also known from a single locality (2 collections) in Jamaica and a single Cuban collection. Crum (1965), in reporting on the Cuban collection (*Ekman 18038*, Viñales, Pinar del Río, FH, MICH), found that it deviated somewhat from the type in having forked stems and incrassate, strongly porose cells throughout the leaves. He considered the Jamaican collections intermediate in form between the plants from Guatemala and Cuba.

2. *Jaegerina scariosa* (Lorentz) Arzeni, Amer. Midl. Naturalist 52: 12. 1954. *Meteorium scariosum* Lorentz, Moosstudien 165. 1864. *Garovaglia scariosa* (Lorentz) Müll. Hal. *in* Broth., Hedwigia 34: 128. 1895. *Pilotrichum scariosum* (Lorentz) Müll. Hal. *ex* Paris, Index Bryol. 956. 1897. *Pterobryopsis scariosa* (Lorentz) M. Fleisch., Hedwigia 45: 60. 1905. *Jaegerinopsis scariosa*

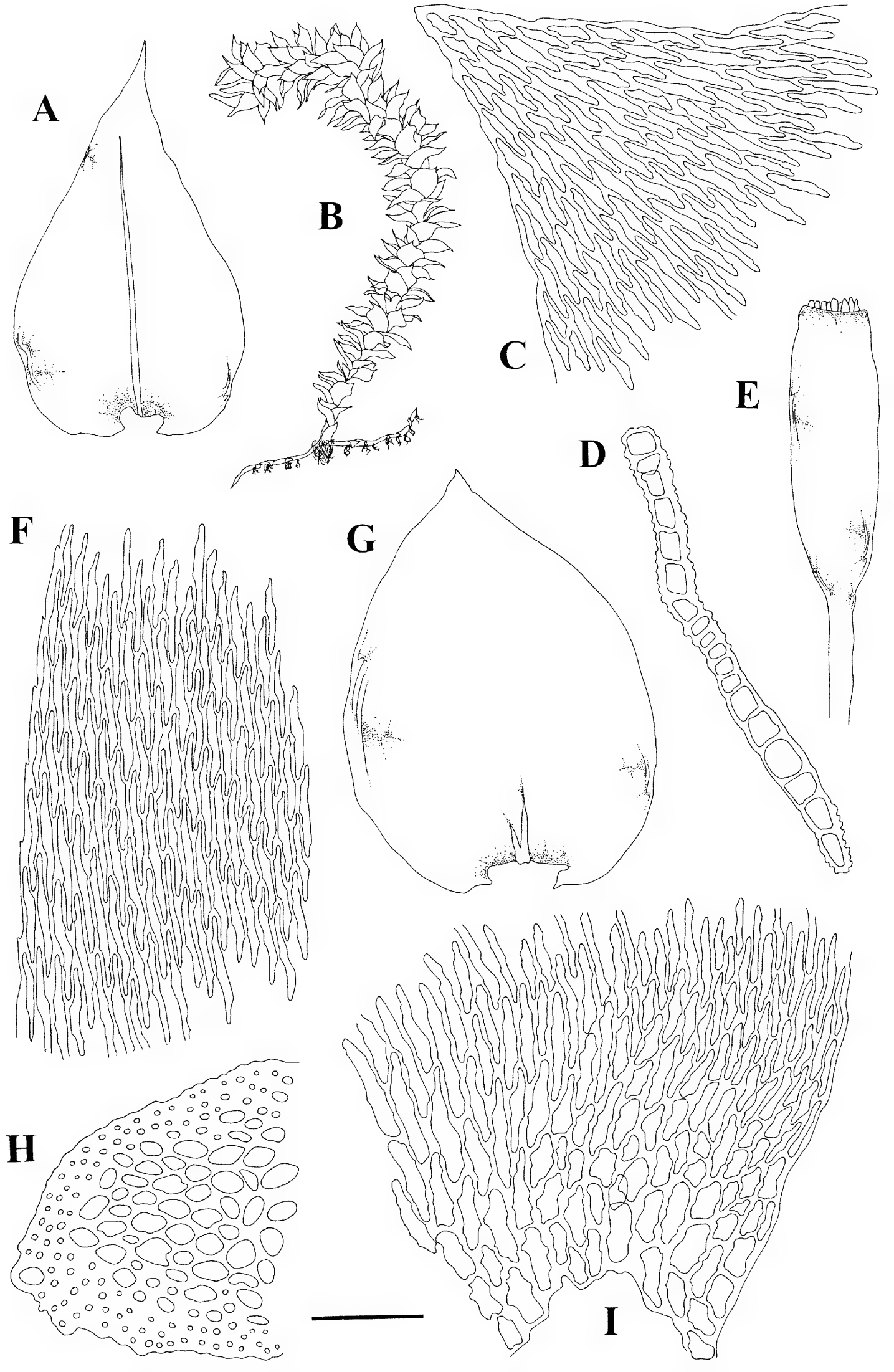


Figure 63. *Jaegerina scariosa*. A & G. Leaves. B. Habit. C. Leaf apex. D. Gemma. E. Seta and capsule. F. Median leaf cells and margin. H. Stem in cross section. I. Basal and alar cells. Scale in mm: bar = 0.06 (C, D, F, H, I); bar = 0.6 (A, G); bar = 0.7 (E); bar = 5.0 (B). A from *Crosby 10805*; D from *Crosby 4330*; all other figure parts from *Allen 12910*.

(Lorentz) Broth., Nat. Pflanzenfam. I(3): 791. 1906. Protologue. Prov. Chiriqui in Panama leg. *M. Wagner* April 1858.

Garovaglia ulei Müll. Hal. *in* Broth., Hedwigia 34: 128. 1895. *Pterobryopsis ulei* (Müll. Hal.) M. Fleisch., Hedwigia 45: 60. 1905. *Jaegerinopsis ulei* (Müll. Hal.) Broth., Nat. Pflanzenfam. I(3): 791. 1906. Protologue. [Brazil] Goyaz: Mossamedes, ad truncos et in ramis arborum sylvestrium ad flumen Rio dos Almas, Januario 1893–*Ule n. 1620, 1572*.

Jaegerinopsis squarrosa E. Britton, Bryologist 21: 48. 1918. Protologue. Sierra de las Yeguas, San Diego de los Baños, Pinar del Rio, Cuba, (*Jaegerinopsis Cubensis* n. sp. MS in Hb), June 28, 1915, South Slope of Sierra de los Helechales, Banao Mts., Santa Clara, *Bros. Leon* and *Clement*, Aug. 1915. Also on Magnolias near Sanford, Florida, *S. Rapp*. 1917. Type. Cuba. Sierra de las Yeguas, near San Diego de los Baños (Pinas del Río), collected by *Bro. León 5239*, June 28 1915 (FH, syntype).

Jaegerinopsis cubensis E. Britton, Bryologist 21: 48. 1918, invalid name, listed in synonymy, based on Sierra de las Yeguas, San Diego de los Baños, Pinar del Rio, Cuba, June 28, 1915 (FH).

Plants small to medium-sized, in green to yellow green, lax tufts or masses on trees. Primary stems creeping, with small, erect to imbricate, distantly spaced leaves; rhizoids red brown, smooth to roughened, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions and at base of secondary stems. Secondary stems irregularly spaced, erect, not stipitate, not or rarely branched, stem tips at times becoming flagellate, 1–4 cm long; stems in cross section with sclerodermis of 3–5 rows of small, reddish yellow, thick-walled cells, cortical cells enlarged, yellowish to hyaline, firm- to thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous; leaves wide-spreading to squarrose, 1–3 mm long, broadly ovate to ovate-lanceolate, acute to broadly acuminate, concave, cordate at base, not or very shortly decurrent; margins entire to lightly serrulate below, serrulate above, plane; costae variable, short, faint and either single or double or single, slender and reaching just beyond midleaf; cells linear-flexuose, smooth, porose and firm-walled throughout, apical cells 32–50 × 4–6 µm, median cells 40–60 × 4–6 µm; basal cells to 70 µm long; alar cells weakly developed, of a few irregularly subquadrate, incrassate cells at the basal angles, cells across the insertions yellow. Asexual reproduction by smooth, hyaline, uniseriate, septate gemmae arising from large, circular clusters of initials in leaf axils, germinating from both ends, new filaments coarsely papillose. Dioicous. Perichaetial leaves sheathing the lower 1/3 of the setae, 2–3 mm long. Setae smooth to lightly roughened below, reddish brown, 4–6 mm long. Capsules erect, symmetric, short-cylindric, 1.5–2.0 mm long; exothecial cells at mouth red, quadrate to oblate, thick-walled, in 6–8 rows, lower exothecial cells short-rectangular, firm-walled; stomata absent; opercula conic-rostrate, 1 mm long; annuli rudimentary, of firm-walled cells; peristome diplolepideous; exostome teeth pale yellow, rudimentary, truncate-triangular, to 100 µm long, smooth to finely roughened, weakly trabeculate, prostome present; endostome absent. Spores round, smooth to lightly papillose, 22–28 µm. Calyptra not seen ("cucullate, naked, slightly roughened," Buck 1998).

Illustrations. Britton (1918, Pl. 24); Brotherus (1925, Fig. 541); Bartram (1949, Fig. 109 G, Fig. 112 G–I); Arzeni (1954, Pl. 2 2 & Pl. 4); Breen (1963, Pl. 108); Argent (1973a, Figs. 9 & 10); Crum and Anderson (1981, Fig. 381); Reese (1984, Fig. 43 K–N); Churchill (1994, Fig. 33 A); Sharp *et al.* (1994, Fig. 524); Churchill and Linares (1995, Fig. 166 e–i); Duarte Bello (1997, Pl. 183); Buck (1998, Pl. 56 1–9); Gradstein *et al.* (2001, Fig. 195 A–E); Buck (2003, Fig. 112). Figure 63.

Habitat. On bark of tree trunks and treelets; 95–900 m.

Distribution in Central America. BELIZE. Cayo: *Allen 18444A* (MO); Toledo: *Gentle 5402* (MO). GUATEMALA. Baja Verapaz: *Sharp 2665a* (FH); Petén: *Lundell 2037* (FH). EL SALVADOR. Santa Ana: *Sipman et al. 37381* (NY). HONDURAS. Atlántida: *Allen 17639* (MO); Comayagua: *Allen 13673* (MO); Copán: *Allen 17711* (MO); Olancho: *Allen 12910* (MO). COSTA RICA. Alajuela: *Jiménez 8* (FH, NY). PANAMA. Canal Area: *Crosby 10805* (MO); Chiriquí: *Crosby 3973* (MO); Colón: *Crosby 10337* (MO); Darién: *Allen 8963A* (MO); Los Santos: *McPherson 13508E* (MO); Panamá: *Crosby 4330* (MO).

World range: Southeastern U.S.A.; Mexico; Central America; Caribbean; Western Northern, and Southern South America, Brazil; West and West-Central Tropical Africa.

Jaegerina scariosa is usually a medium-sized species with erect, mostly unbranched, secondary stems. Its leaves are wide-spreading to squarrose, they vary in shape from broadly ovate to ovate-

lanceolate, and they have very weakly developed alar cells. The leaf costae in *J. scariosa* are remarkably variable, and sometimes leaves from a single stem can have short, double or long, single costae. In view of its inconsistency, the value of this character as a taxonomically important feature appears questionable. There are, however, two fairly distinct forms of *J. scariosa* in Central America, one with broadly ovate leaves and mostly short, double costae, the other with ovate-lanceolate leaves and mostly long, single costae. The former represents the type concept of *J. scariosa*, the latter the type concept of *J. squarrosa*. Argent (1973a) synonymized the African species of *Jaegerina* with *J. scariosa*, but he noted that unlike the American collections, in African material the costa was ". . . uniformly present, single and well developed."

Jaegerina guatemalensis differs from *J. scariosa* in having narrower, long-acuminate leaves with subpercurrent costae. *Renauldia mexicana* is similar to the ecostate to short-double costate form of *J. scariosa* in having non-ranked concave leaves and very weakly developed alar cells. It, however, is a much larger plant than *J. scariosa*, with irregularly pinnately branched stems and erect to imbricate leaves. In addition, *R. mexicana* does not have asexual axillary gemmae. There are some *Pireella* species with concave leaves and weakly developed alar cells that are similar to the single costate form of *J. scariosa*. They differ from *J. scariosa* in having stipitate secondary stems that are frondose to pinnately branched and erect to spreading leaves that are often in spiral rows.

4. *Orthostichidium* Müll. Hal. *ex* Dusén, Kongl. Svenska Vetenskapsakad. Handl. 28(2): 19. 1895.

Plants medium-sized to robust, in loose or dense mats. Primary stems creeping, with erect to imbricate, distantly spaced leaves; rhizoids from clusters of initials at abaxial side of primary stem leaf insertions and at base of stipes. Secondary stems irregularly spaced, erect, stipitate, irregularly pinnate branched, branches at times becoming flagellate; stems in cross section with sclerodermis present, cortical cells enlarged, firm- to thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous; leaves loosely erect-spreading in more or less spiral rows when dry, erect to imbricate in distinct spiral rows when wet, oblong-ovate, acute to short-acuminate, at times more or less cuspidate, concave, cordate to subauriculate at base, shortly decurrent; margins entire throughout or lightly serrulate at the apex, broadly incurved above; costae absent or short, faint and double; cells linear-flexuose, porose and firm-walled throughout; alar cells red to reddish yellow, weakly developed, rhombic to short-rectangular, cells across the leaf insertions red. Branch leaves smaller and less cordate at base than secondary stem leaves, otherwise similar to secondary stem leaves. Asexual reproduction by smooth, hyaline to yellowish, uniseriate, septate gemmae arising from large, circular cluster of initials in leaf axils; gemmae becoming secondarily elongate, cells smaller and papillose. Dioicous. Perichaetia and perigonia lateral on stems and branches. Setae short, smooth. Capsules immersed, erect, symmetric, oblong-ovoid; stomata absent; opercula conic-rostrate; annuli rudimentary; peristome diplolepideous, prostome well developed; exostome teeth pale yellow, narrowly triangular, smooth to finely roughened, weakly trabeculate; endostome rudimentary, basal membranes low, segments short, cilia absent. Calyptrae mitrate, naked, smooth.

Orthostichidium is a genus of three species found in Africa (*O. pentasticum* (Brid.) B. H. Allen & Magill and *O. involutifolium* (Mitt.) Broth.) and the Neotropics (*O. quadrangulare*). The genus has stoloniferous primary stems and stipitate secondary stems with spirally ranked (especially when wet) leaves. The acute to shortly cuspidate leaves of *Orthostichidium* are ecostate (or have a very short, double costa), and rounded or cordate at the insertions. The leaf cells in *Orthostichidium* are smooth, linear-flexuose, and often porose, while the alar cells are very weakly developed. *Orthostichidium* has immersed, oblong-ovoid capsules, conic-rostrate opercula, and mitrate calyptrae.

Argent (1973b) regarded *Orthostichidium* to be very close to *Hildebrantiella* Müll. Hal., which is usually distinguished from *Orthostichidium* by its better-developed alar cells, cucullate calyptrae, long, cylindrical capsules, and longer-beaked opercula. Buck (1991) considered these differences insufficient in distinguishing the two genera and synonymized them. Although the sporophytic differences noted above are not sufficient to recognize two genera (*e.g.*, the entire range of features can be seen in *Calyptothecium*), these differences in conjunction with their very different alar cell development do support the continued recognition of *Orthostichidium* and *Hildebrantiella*. In *Hildebrantiella* the alar cells are extensively developed in enlarged, more or less inflated groups, while the alar cells

of *Orthostichidium* are nearly undifferentiated. Furthermore, although Argent (1973b) described *Hildebrantiella* as having leaves "often spirally ranked," none of the material of *Hildebrantiella* examined at MO has spirally ranked leaves. *Orthostichidium* appears to be more closely related to *Renauldia* than to *Hildebrantiella. Orthostichidium* has sporophytes identical to those of *Renauldia*, and their leaves are mostly ecostate and similarly shaped, with very weakly developed alar cells. Indeed, the only difference between the two genera is the presence of spirally ranked leaves in *Orthostichidium* and evenly foliate leaves in *Renauldia.*

The name *Orthostichidium* combines the Greek *orthos* (straight) and *stichos* (row) with the suffix *-idium* (indicating diminutive) and refers to the characteristically ranked leaves of the genus.

Orthostichidium quadrangulare (Schwägr.) B. H. Allen & Magill, Bryologist 110: 36. 2007. *Hypnum quadrangulare* Schwägr., Sp. Musc. Frond., Suppl. 1(2): 211. 1816. Protologue. [French Guiana] Ad arborum truncos in Guyana legit *Claudius Richard*, Professor botan. Parisinus. Type (see Allen & Magill 2007). *Hypnum quadrangulare* a Rich. s.n. [element A] (G, lectotype). Not *Hypnum quadrangulare* a Rich. s.n. [element B] (G). Not "*Hypnum quadrangulare*" Schw.! in Herb. Richard–Guyana (*Richard*) (BM).

Neckera guyanensis Mont., Syll. Gen. Sp. Crypt. 24. 1856. *Meteorium guyanense* (Mont.) Mitt., J. Linn. Soc., Bot. 12: 430. 1869 ["*guianense*"]. *Pilotrichella guyanensis* (Mont.) Paris, Index Bryol. 945. 1895. *Orthostichidium guyanense* (Mont.) Broth., Nat. Pflanzenfam. I(3): 795. 1906. *Hildebrantiella guyanensis* (Mont.) W. R. Buck, Brittonia 43: 97. 1991. Protologue. [French Guiana] Ad ramulos in sylvis umbrosis Guyanae: *Leprieur*.

Meteorium excavatum Mitt., J. Linn. Soc, Bot. 12: 430. 1869. *Pilotrichella excavata* (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 254. 1877. *Orthostichidium excavatum* (Mitt.) Broth., Nat. Pflanzenfam. I(3): 795. 1906. Protologue. [Colombia] Absque loco indicato, *Humboldt* in Herb. Hooker. Andes Bogotenses, *Weir, n. 417, 420*. Type (see Florschütz 1964). Andes Bogotenses, leg. *Weir N° 417* [Herb. Mitten] (S, isolectotype).

Pilotrichum pentagonum Hampe & Lorentz *in* Hampe, Bot. Zeitung (Berlin) 27: 449. 1869. *Pilotrichella pentagona* (Hampe & Lorentz) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 257. 1877. *Orthostichidium pentagonum* (Hampe & Lorentz) Müll. Hal., Bull. Herb. Boissier 5: 205. 1897. *Hildebrantiella pentagona* (Hampe & Lorentz) Paris, Index Bryol. Suppl. 181. 1900. Protologue. Hab. Ecuador [Prov. Loja], ad truncos in sylv. Timbara, 3400′, [*H. Krause*].

Plants medium-sized to robust, in green to yellow green, loose or dense mats. Primary stems creeping, with erect to imbricate, distantly spaced leaves; rhizoids red brown, roughened, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions and at base of stipes. Secondary stems irregularly spaced, erect, stipitate, irregularly pinnate-branched, branches at times becoming flagellate, or transformed to stoloniferous stems, 4–15 cm long; stems in cross section with sclerodermis of 4–6 rows of small, reddish yellow, thick-walled cells, cortical cells enlarged, yellowish to hyaline, firm- to thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous; leaves loosely erect-spreading in more or less spiral rows when dry, erect to imbricate in distinct spiral rows when wet, 1.5–3.0 mm long, oblong-ovate, acute to short-acuminate, at times more or less cuspidate, concave, cordate to subauriculate at base, shortly decurrent; margins entire throughout or lightly serrulate at the apex, broadly incurved above; costae absent or short, faint, and double; cells linear-flexuose, porose and firm-walled throughout, apical cells 20–40 × 6–8 μm, median cells 40–70 × 3–5 μm; basal cells 50–98 × 3–6 μm; alar cells red to reddish yellow, weakly developed, rhombic to short-rectangular in 2–5 rows, cells across the leaf insertions red. Branch leaves smaller and less cordate at base than secondary stem leaves, otherwise similar to secondary stem leaves. Asexual reproduction by smooth, hyaline to yellowish, uniseriate, septate, often clavate gemmae arising from large, circular cluster of initials in leaf axils; gemmae becoming secondarily elongate, cells smaller and papillose-roughened. Dioicous. Setae short, smooth, 0.5–1.0 mm long. Capsules immersed, erect, symmetric, oblong-oval, 2–3 mm long; exothecial cells oblate in 8–10 rows at mouth, short-rectangular to subquadrate, firm-walled below; stomata absent; opercula conic-rostrate, 0.4–0.5 mm long; annuli rudimentary; peristome diplolepideous, prostome well developed; exostome teeth pale yellow, narrowly triangular, smooth to finely roughened, weakly trabeculate; endostome rudimentary, basal membranes low, segments short, cilia absent. Spores rounded to oblong, smooth to lightly roughened, 24–40 μm long. Calyptra not seen, "mitrate, naked, smooth" (Buck 1998).

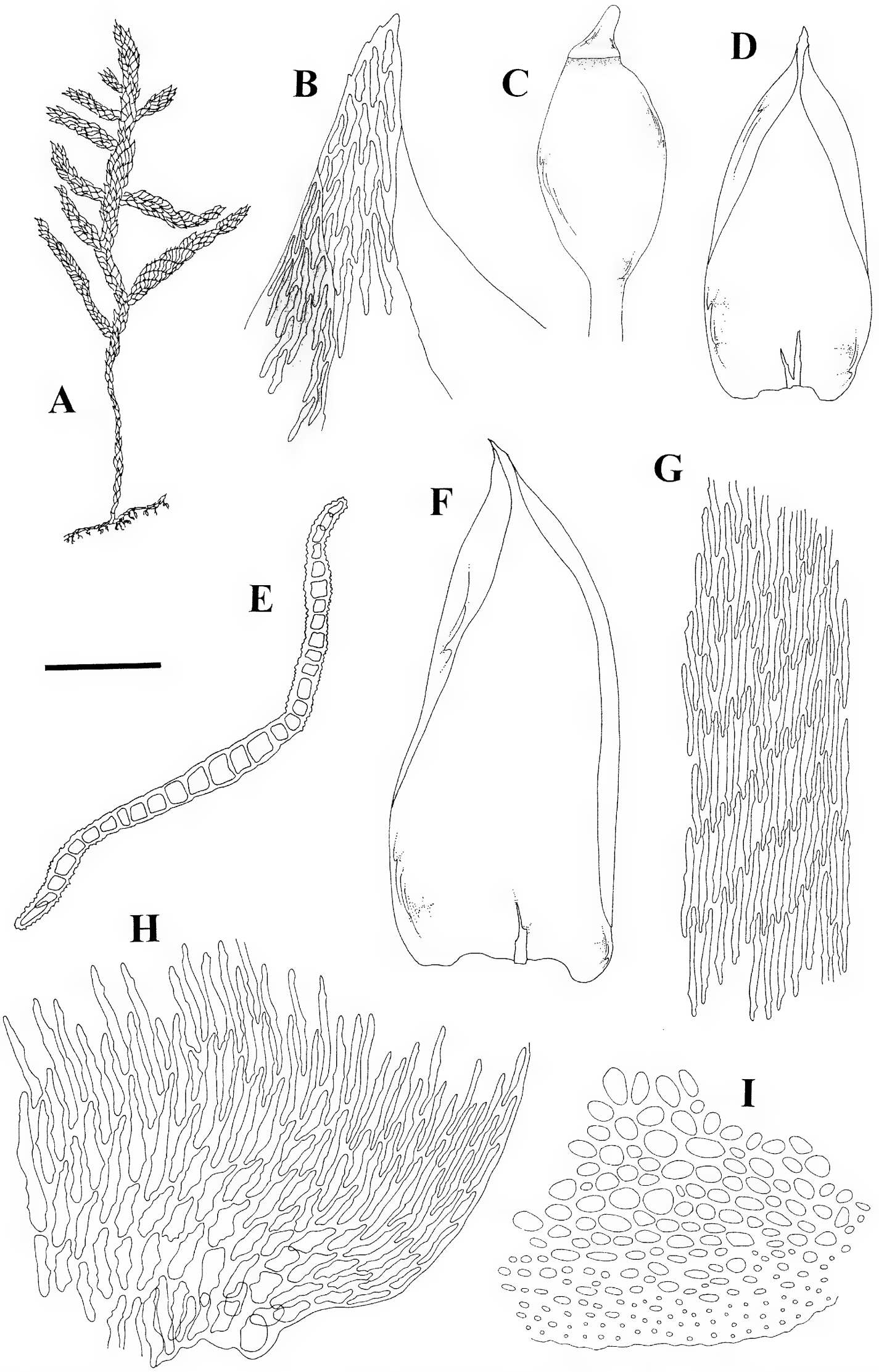
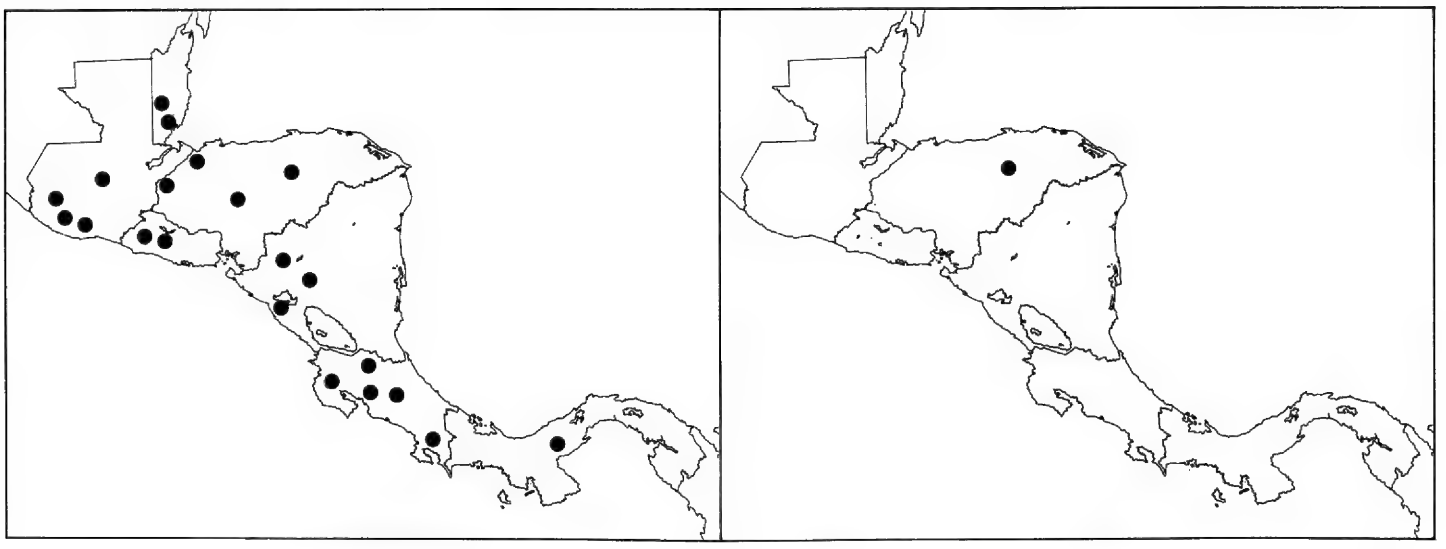


Figure 64. *Orthostichidium quadrangulare*. A. Habit. B. Leaf apex. C. Seta and capsule. D. Branch leaf. E. Gemma. F. Stem leaf. G. Median leaf cells. H. Basal and alar cells. I. Stem in cross section. Scale in mm: bar = 0.05 (E); bar = 0.06 (B, G, H); bar = 0.08 (I); bar = 0.5 (D, F); bar = 0.8 (C); bar = 4.0 (A). C from *Standley 63393*; E from *Zardini 60747*; all other figure parts from *Allen 12913*.



Orthostichidium quadrangulare *Orthostichopsis fornicata*

Illustrations. Bartram (1949, Fig. 113 F–G, Fig. 124 A–B); Arzeni (1954, Pl. 1); Churchill (1994, Fig. 35 C–D); Sharp *et al.* (1994, Fig. 525); Churchill and Linares (1995, Fig. 166 a–c); Duarte Bello (1997, Pl. 184); Buck (1998, Pl. 60 1–7); Gradstein *et al.* (2001, Fig. 194 I–K). Figure 64.

Habitat. Epiphyte on tree trunks, in crowns of trees, on vines fallen from the canopy, and on fences, rarely on rocks; 455–1800 m.

Distribution in Central America. BELIZE. Cayo: *Allen 15134* (MO); Toledo: *Allen 18495* (MO). GUATEMALA. Baja Verapaz: *Sharp 2665* (FH); Escuintla: *Standley 63393* (F, FH); Quetzaltenango: *Bauer s.n.* (FH); Suchitepéquez: *Kellerman s.n.* (FH, US). EL SALVADOR. Cuscatlán: *Calderón 1996a* (NY, US); Sonsonate: *Kovar 30* (MICH). HONDURAS. Comayagua: *Allen 13673A* (MO); Copán: *Allen 17684* (MO, TEFH); Cortés: *Morton 7865* (US); Olancho: *Allen 12786* (MO, TEFH). NICARAGUA. Estelí: *Stevens & Henrich 20263* (HNMN, MO); Managua: *Standley 8152* (F, FH); Matagalpa: *D'Arcy s.n.* (F, MO). COSTA RICA. Alajuela: *Brenes 16694* (F, NY); Cartago: *Liesner & Judziewicz 14564* (MO); Guanacaste: *Standley & Valerio 45240* (FH, NY, US); Puntarenas: *Gómez 25409* (MO); San José: *Griffin & Morales C 145* (F, MO, NY). PANAMA. Coclé: *Hunter & Allen 343A* (MO).

World range: Mexico; Central America; Caribbean; Western, Northern, and Southern South America, Brazil.

Orthostichidium quadrangulare is a medium-sized to robust species with stipitate secondary stems that are irregularly pinnately branched. Its leaves are loosely erect when dry and more or less arranged into spiral rows. When wet, however, the leaves are erect-imbricate and occur in sharply defined spiral rows. The leaves of *O. quadrangulare* are cordate at base and most are ecostate; however, some leaves with short, double costae can nearly always be found. The leaf cells are linear-flexuose, smooth, and porose, and the alar cells are reddish but otherwise weakly differentiated. The presence of multicellular, uniseriate gemmae clustered in the leaf axils is a fairly constant feature of the species. The gemmae are smooth and often clavate in shape, but after detaching they elongate at both ends and the new cells are commonly papillose-roughened. This gemmae feature is also seen in *Pterobryopsis mexicana.* Important sporophytic features of *O. quadrangulare* include its immersed capsules, rudimentary annuli, and diplolepideous peristomes with well-developed prostomes.

Florschütz (1964) found the type of *Hypnum quadrangulare* consisted of a mixture of *Pireella pohlii* and *Orthostichidium guyanense*. The description of *H. quadrangulare* calls for plants with 4-ranked leaves (an *Orthostichidium* feature) that have percurrent costae and exserted capsules (*Pireella* features). Since the description of *H. quadrangulare* was based on both elements of the type, Florschütz rejected the name. The type specimen in G consists of two separate and distinct elements: element A is *O. guyanense*; element B is *P. pohlii*. Element A was chosen by Allen and Magill (2007) as the type of *H. quadrangulare*. There is a duplicate of the type specimen in BM from the Wilson Herbarium, which consists of only *P. pohlii*. Apparently, there is also another part of the type collec-

tion of *H. quadrangulare* at BM, which I have not seen, but which Florschütz (1964) cited under *Orthostichidium guyanense.*

Dry plants of *Renauldia mexicana* can be difficult to distinguish from *O. quadrangulare*, because the species are similar in size and have stipitate secondary stems that are irregularly pinnately branched and similar in aspect. Both species also have similarly shaped, more or less ecostate leaves that are cordate at base and have weakly developed alar cells. *Renauldia mexicana* differs from *O. quadrangulare* in having leaves that are more broadly acute and unranked when wet (wet leaves strongly spirally ranked in *O. quadrangulare*). Furthermore, *R. mexicana* appears to lack axillary asexual gemmae.

Orthostichopsis tetragona is sometimes confused with *Orthostichidium quadrangulare*, because both species have spirally ranked, broadly acute to cuspidate leaves that are more or less similar in size. In *Orthostichopsis tetragona*, however, the plants are often pendent and the secondary stems are typically not or weakly branched. Furthermore, the secondary stem and branch leaves of *O. tetragona* are plicate and strongly spirally ranked when either wet or dry. Microscopically, *Orthostichopsis tetragona* differs from *Orthostichidium quadrangulare* in having mostly costate leaves with extensively developed alar cells.

Argent (1973b) and Buck (1998) considered the African *Orthostichidium involutifolium* (Mitt.) Broth. and *O. quadrangulare* (as *O. pentagonum* or *O. guyanese*) to be gametophytically very close and perhaps synonymous. Buck (1998) noted that *O. involutifolium* was somewhat different in aspect from *O. quadrangulare*, apparently due to its smaller size and stem leaves that are more distinctly ranked.

5. *Orthostichopsis* Broth., Nat. Pflanzenfam. I(3): 804. 1906.

Plants medium-sized to robust, brownish green, in dense, pendent masses. Primary stems creeping, with erect to imbricate leaves; rhizoids red brown, smooth, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions, but also on abaxial side of leaves on transformed secondary stem and branch tips; leaves not spirally arranged, erect, oblong-ovate, hair-pointed, concave, decurrent; margins serrulate throughout, plane to lightly incurved; costae variable, at times absent or short and double, but usually single and ending above midleaf; leaf cells linear to linear-flexuose, smooth, firm- or thick-walled, porose, reddish yellow across the base; alar cells variously differentiated. Secondary stems more or less turgid, irregularly branched, not stipitate, stems and branches often transformed to stoloniferous stems at the tips; stems in cross section with sclerodermis, enlarged, thick-walled cortical cells, central strand absent, paraphyllia absent; pseudoparaphyllia filamentous; leaves erect to erect-spreading, little altered when dry, at times strongly seriately ranked, oblong-lanceolate, ovate-lanceolate, or broadly oblong-ovate, smooth or plicate, abruptly long-cuspidate to hair-pointed, deeply concave, rounded to more or less cordate at base; margins plane below, broadly incurved above at base of cusp, entire to subentire below, subentire to serrulate above; costae single, slender, mostly reaching 3/4 the leaf length, in cross section with 2 layers of thick-walled cells; leaf cells smooth, very thick-walled, porose, rhomboidal to linear-fusiform, becoming broader toward the insertion, cells across the leaf base red to red yellow in a broad band. Branch leaves erect-spreading, in distinct seriate rows, broadly oblong to oblong-ovate, abruptly long-cuspidate to hair-pointed, concave, rounded to the insertion; margins plane below, incurved above, serrulate in the cusp, serrulate to subentire below; costae slender, often yellow, ending near or just above midleaf; upper and median cells similar to secondary stem leaves; alar cells variously differentiated. Dioicous. Perichaetia and perigonia lateral on secondary stems and branches. Vaginulae with uniseriate, crispate hairs. Setae long or short, smooth. Capsules immersed to exserted, broadly oval to oblong-cylindric; exothecial cells oblate near the mouth, short-rectangular below; stomata absent; opercula conic-rostrate; annuli rudimentary; peristome diplolepideous, inserted within the mouth; exostome teeth smooth; prostome well developed; endostome rudimentary and adhering to the exostome teeth. Spores ovoid to oblong, large, finely roughened. Calyptrae cucullate, pilose with long, crispate, 1–3-seriate hairs.

Orthostichopsis is a genus of 19 species found in the tropical regions of America and Africa. Its plants often have a pendent growth form and lack stipitate secondary stems, which Buck (1998) noted

gave the genus the most "Meteoriaceae-like habit" of any genus in the Pterobryaceae. *Orthostichopsis* is placed in the Pterobryaceae on the strength of its numerous filamentous pseudoparaphyllia and well-developed peristomial prostome. Most species of *Orthostichopsis* have spirally ranked branch leaves, but at least one species (*O. tortipilis* (Müll. Hal.) Broth.) has leaves that are weakly or not ranked. Other important features of the genus include its apparent lack of asexual propagula; long, single costae; usually well-developed alar cells; linear-flexuose, thick-walled, and porose leaf cells; densely hairy vaginulae; cylindrical capsules; and cucullate calyptrae that are densely covered by long, crispate hairs.

Orthostichopsis species are superficially very similar to those of *Squamidium* or *Orthostichella*. The resemblance to *Squamidium* is due to its pendent habit, spirally ranked leaves, single costae, and well-differentiated alar cells. *Squamidium* differs from *Orthostichopsis* in often having a blackish coloration, scale leaves rather than filamentous pseudoparaphyllia over the branch buds, weaker costae, absence of a region of red cells across the leaf bases, strongly decurrent leaves, and better-developed endostomes. Plants of *Orthostichella* are also similar to *Orthostichopsis* in having a pendent habit and spirally ranked leaves. *Orthostichella* differs from *Orthostichopsis* in often having plants with deciduous leaves; leaves ecostate or with weak, short, double or single, inconsistently developed costae; and stems that have either foliose pseudoparaphyllia or scale leaves over the branch buds. The sporophytes and related structures of *Orthostichella* differ from those of *Orthostichopsis* in having ovoid to short-cylindrical capsules with superficial stomata; peristomes that lack prostome development but have well-developed endostomes; small spores; and smooth to lightly hairy calyptrae.

The American species of *Orthostichopsis* were treated by Buck (1991). Argent (1973a) reviewed the mainland African species of *Orthostichopsis*, but the greatest African diversity in the genus occurs in Madagascar and the Mascarene Islands.

The name *Orthostichopsis* combines the Greek *orthos* (straight), *stichos* (row), and *opsis* (aspect, appearance) and refers to the characteristically ranked leaves of the genus.

1. Branch leaves plicate, mostly cuspidate; alar cells in 15–30 rows along the basal margins . . . . 3. *O. tetragona*
1. Branch leaves concave, not plicate, long-cuspidate to hair-pointed; alar cells in 2–8 rows along the basal margins 2
2. Branch leaf alar cells in 2–3 rows along the basal margins; setae 4.0 mm long . . . . . 1. *O. fornicata*
2. Branch leaf alar cells in 4–8 rows along the basal margins; setae 0.5 mm long . . . . . 2. *O. praetermissa*

1. *Orthostichopsis fornicata* B. H. Allen & W. R. Buck, *sp. nov.* Type. Honduras. Olancho: Sierra de Algalta; La Chorrera, Rio Lara below Montana Bibilonia, 15 km NNW of Catacamas, 14°59′N, 85°56′W, 1100–1800 m, *Allen 12548* (MO, holotype; B, BM, DUKE, FH, H, JE, NY, S, TEFH, US, isotypes).

Species haec *O. praetermissae* affinis sed cellulis alaribus vix evolutis setisque elongatis differt.

Plants medium-sized to robust, brownish green, in dense, pendent masses. Primary stems creeping, with erect to imbricate leaves; rhizoids red brown, smooth, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions, but also on abaxial side of leaves on transformed secondary stem and branch tips; leaves not spirally arranged, erect, oblong-ovate, 1.0–1.5 mm long, hair-pointed, concave, decurrent; margins serrulate throughout, plane to lightly incurved; costae variable, at times absent or short and double, but usually single and ending above mid-leaf; leaf cells linear to linear-flexuose, smooth, firm- or thick-walled, porose, reddish yellow across the base; alar cells weakly differentiated, of a few subrectangular, very thick-walled and porose cells. Secondary stems more or less turgid, to 20 cm long, irregularly branched, stems and branches often transformed to stoloniferous stems at the tips; stems in cross section with sclerodermis of 4–6 rows of small, reddish yellow, thick-walled cells, cortical cells enlarged, yellowish to hyaline, firm- to thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous; leaves erect to erect-spreading, little altered when dry, not seriately arranged, broadly oblong to broadly oblong-ovate, abruptly long-cuspidate to hair-pointed, 1.6–2.0 mm long, cusp 0.4–0.7 mm long, deeply concave, rounded to more or less cordate at base; margins plane below, broadly incurved above at base of cusp, entire to subentire below, subentire to serrulate above; costae single, slender, mostly reach-

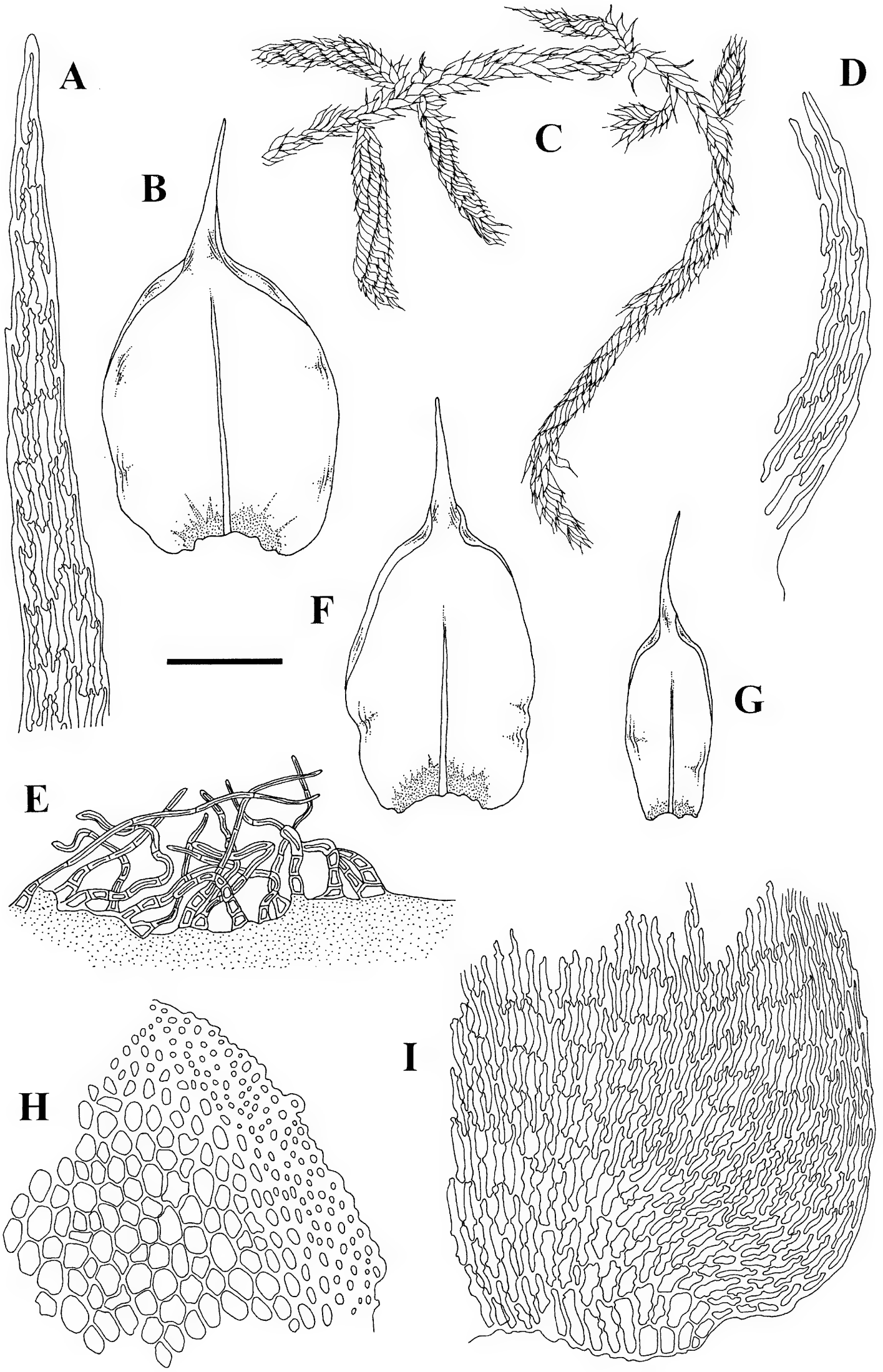


Figure 65. *Orthostichopsis fornicata*. A. Leaf apex. B & F. Stem leaves. C. Habit. D. Median leaf cells and margin. E. Pseudoparaphyllia. G. Branch leaf. H. Stem in cross section. I. Basal and alar cells. Scale in mm: bar = 0.05 (E); bar = 0.06 (A, D, H, I); bar = 0.5 (B, F, G); bar = 6.4 (C). All figure parts from *Allen 12548*.

ing 3/4 the leaf length, in cross section with 2 layers of thick-walled cells, ventral layer enlarged; leaf cells smooth, very thick-walled, porose, linear-fusiform, 35–55 × 3 μm, toward base 6–8 μm wide; cells across the leaf base red to red yellow in a broad band; alar cells weakly differentiated, thick-walled, porose, in 2–3 rows along the basal margin, extending inward 4–6 cells, subquadrate at the margins, short-rectangular intramarginally. Branch leaves erect-spreading, in distinct seriate rows, broadly oblong to oblong-ovate, abruptly long-cuspidate to hair-pointed, 1.2–1.5 mm long, cusp 0.4 mm long, concave, rounded to the insertion; margins plane below, incurved above, serrulate in the cusp, serrulate to subentire below; costae slender, often yellow, ending near or just above midleaf; upper and median cells similar to secondary stem leaves; alar cells nearly undifferentiated. Dioicous. Unfertilized perichaetia lateral on secondary stems and branches, 1 mm long; archegonia numerous; paraphyses long, narrow-celled. Fertilized perichaetial leaves oblong-lanceolate, gradually to abruptly long-loriform, 2 mm long; margins subentire to serrulate above; alar cells undifferentiated. Vaginulae densely hairy; hairs uniseriate, crispate. Setae at least 4.0 mm long, reddish, smooth. Capsules and opercula unknown. Immature calyptrae densely hairy.

Illustration. Figure 65.
Habitat. Pendent on tree trunks, canopy branches, and vines; 1000–1800 m.
Distribution in Central America. HONDURAS. Olancho: *Allen 12419* (MO).
World range: Central America.

Orthostichopsis fornicata is a medium-sized to robust species found at generally higher elevations than the other Central American species of *Orthostichopsis*. The secondary stem leaves in *O. fornicata* are larger than the branch leaves and not ranked in seriate rows; otherwise, the leaves are more or less similar in shape and both are long-cuspidate to hair-pointed. The leaf cells are remarkably thick-walled and porose throughout, and the alar cells are hardly differentiated. In fact, the alar cells in most of the branch leaves are only slightly shorter and wider than the basal leaf cells near the costa. The type collection of *O. fornicata* contains several plants with elongate setae, on which the capsules are missing. The length of these setae, however, indicates the capsules were exserted.

Orthostichopsis praetermissa is gametophytically very similar to *O. fornicata*. Both species have long-cuspidate to hair-pointed secondary stem and branch leaves and concave, non-plicate branch leaves. *Orthostichopsis praetermissa* differs from *O. fornicata* in having better-developed alar cells (in 4–8 vs. 2–3 rows along the basal margins) and shorter setae (0.5 mm vs. 4.0 mm). The alar cell differences between these two species are especially pronounced in their branch leaves. In *O. praetermissa* the branch leaf alar cells are differentiated in a manner more or less similar to those of the secondary stem leaves, while in *O. fornicata* they are nearly undifferentiated.

Orthostichopsis tetragona differs from *O. fornicata* in having very well-developed alar cells (in 15–30 rows along the basal margin), plicate, mostly cuspidate branch leaves, and shorter (0.5–0.8 mm long) setae.

2. *Orthostichopsis praetermissa* W. R. Buck, Brittonia 43: 98. 1991. Protologue. Peru. Infra verticem montis Guayrapurina ad arborum ramulos [3000 m], Sep 1856, *Spruce 1207* (NY, holotype).

Plants medium-sized to robust, brownish green, in dense, often pendent masses. Primary stems creeping, with erect to imbricate leaves; rhizoids red brown, smooth, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions, but also on abaxial side of leaves on transformed secondary stem and branch tips; leaves not spirally arranged, erect, oblong-ovate, 1.0–1.5 mm long, hair-pointed, concave, decurrent; margins subentire throughout, plane to lightly incurved; costae variable, at times absent or short and double, but usually single and ending above midleaf; leaf cells linear to linear-flexuose, smooth, firm- or thick-walled, porose, reddish yellow across the base; alar cells differentiated in 4–8 rows along the basal margins. Secondary stems at times somewhat turgid, to 30 cm long, irregularly branched, secondary stems and branches often transformed to stoloniferous stems at the tips; stems in cross section with sclerodermis of 4–6 rows of small, reddish yellow, thick-walled cells, cortical cells enlarged, yellowish to hyaline, firm- to thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous; leaves erect to erect-spreading, little altered when dry, not seriately arranged, oblong to oblong-ovate, abruptly long-cuspidate to hair-

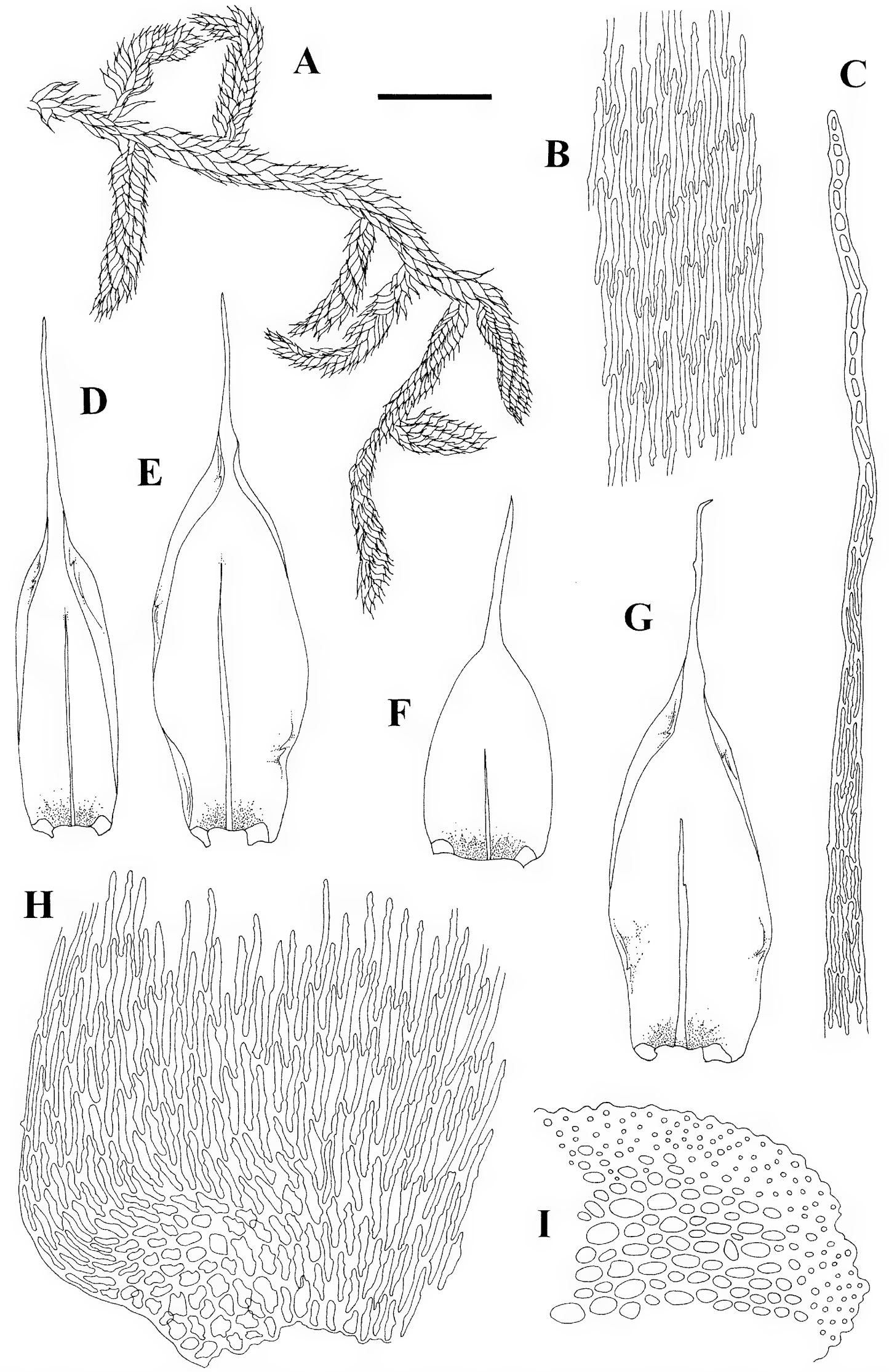
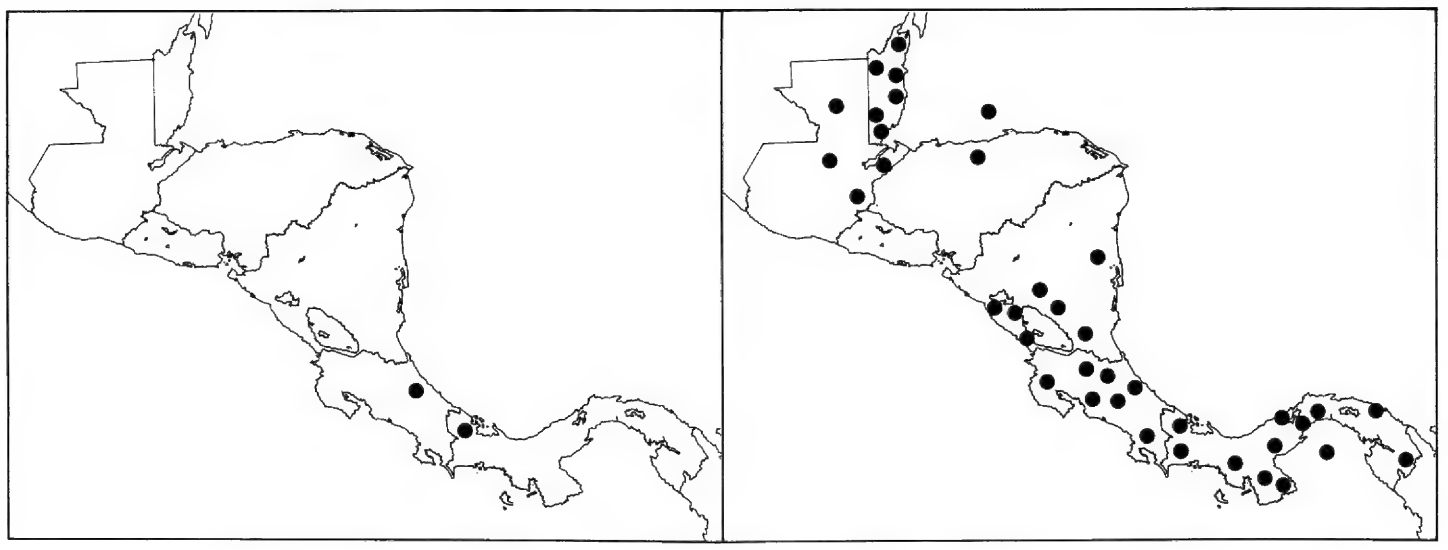


Figure 66. *Orthostichopsis praetermissa*. A. Habit. B. Median leaf cells. C. Leaf hair-point. D. Branch leaf. E & G. Secondary stem leaves. F. Primary stem leaf. H. Basal and alar cells. I. Stem in cross section. Scale in mm: bar = 0.06 (B, H, I); bar = 0.1 (C); bar = 0.5 (D–G); bar = 501 (A). All figure parts from *Allen 5533*.



Orthostichopsis praetermissa *Orthostichopsis tetragona*

pointed, 2.0–2.5 mm long, hair-point 0.5–0.8 mm long, concave, rounded to more or less cordate at base; margins plane or narrowly incurved below, broadly incurved above at base of hair-point, subentire below, subentire to serrulate above; costae single, slender, mostly reaching 3/4 the leaf length, in cross section with 2 layers of thick-walled cells, ventral layer enlarged; leaf cells smooth, firm-walled, porose, linear-fusiform, 40–60 × 3–4 μm, becoming broader toward the base; cells across the leaf base red to red yellow in a broad band; alar cells strongly thickened, strongly porose, in 4–8 rows along the basal margin, extending inward 4–8 cells. Branch leaves erect-spreading, in distinct seriate rows, broadly oblong to oblong-ovate, abruptly long-cuspidate to hair-pointed, 1.7–2.5 mm long, concave, rounded to the insertion; margins plane below, incurved above, serrulate in the cusp, serrulate to subentire below; costae slender, often yellow, ending 1/2–3/4 the leaf length; cells similar to secondary stem leaves. Sporophytes unknown from Central America, description from Buck (1998). Dioicous. Perichaetia conspicuous, leaves lanceolate, 7 mm long, gradually acuminate. Vaginulae crispate-hairy. Setae 0.5 mm long, smooth. Capsules immersed, broadly cylindric, 3 mm long; exothecial cells oblate near the mouth, short-rectangular below; opercula conic-rostrate, 1 mm long; peristome inserted within the mouth; exostome teeth smooth, prostome well developed; endostome rudimentary and adhering to the exostome teeth. Spores ovoid to oblong, 48–69 μm long, finely roughened. Calyptrae cucullate, pilose, with long, crispate, 1–3-seriate hairs.

Illustrations. Buck (1991, Figs. 1–11); Churchill (1994, Fig. 35 A–B); Churchill and Linares (1995, Fig. 167 a–d); Buck (1998, Pl. 59); Buck (2003, Fig. 113). Figure 66.

Habitat. On upper branches of fallen trees; 250–300 m.

Distribution in Central America. COSTA RICA. Limón: *Crosby 3676* (MO). PANAMA. Bocas del Toro: *Allen 5533* (MO).

World range: Central America; Caribbean; Western and Northern South America, Brazil.

Orthostichopsis praetermissa is a medium-sized to robust species with hair-pointed, non-plicate stem and branch leaves. The primary and secondary stem leaves of *O. praetermissa* when dry are typically evenly foliate, but sometimes when wet the secondary stem leaves are spirally ranked. The branch leaves are spirally ranked whether wet or dry. Microscopically, *O. praetermissa* is marked by its rounded to cordate leaf bases that have well-developed alar cells in 4–8 rows at the basal margins. Although the sporophytes of *O. praetermissa* have not been found in Central America, they are immersed.

Central American collections of *O. praetermissa* were previously determined as the Venezuelan species *O. auricosta* (Müll. Hal.) Broth. In describing *O. praetermissa* Buck was unable to locate the type of *O. auricosta*, but since the protologue described the leaves as short-pointed he considered the two unlikely to be the same thing. Plants of *O. praetermissa*, however, nearly always have some stems and branches with cuspidate rather than hair-pointed leaves, and Buck (1991) noted at least one col-

lection having "almost all branch leaves cuspidate rather than aristate." It may be that an examination of the type of *O. auricosta* will show it to be the same as *O. praetermissa*.

Orthostichopsis fornicata is gametophytically nearly identical to *O. praetermissa*, and, in fact, when sporophytes are absent they cannot be separated without microscopic examination. Both species have long-cuspidate to hair-pointed secondary stem and branch leaves, and concave, non-plicate branch leaves. *Orthostichopsis fornicata* differs from *O. praetermissa* in having very weakly developed alar cells (in 2–3 vs. 4–8 rows along the basal margins) and longer setae (4.0 mm vs. 0.5 mm). The alar cell differences between these two species are especially pronounced in their branch leaves. In *O. praetermissa* the branch leaf alar cells are differentiated in a manner more or less similar to those of the secondary stem leaves, while in *O. fornicata* they are nearly undifferentiated.

Orthostichopsis tetragona differs from *O. praetermissa* in having very well-developed alar cells (in 15–30 rows along the basal margin) and plicate, mostly cuspidate branch leaves.

3. *Orthostichopsis tetragona* (Hedw.) Broth., Nat. Pflanzenfam. I(3): 805. 1906. *Hypnum tetragonum* Hedw., Sp. Musc. Frond. 246. 1801. *Isothecium tetragonum* (Hedw.) Brid., Bryol. Univ. 2: 377. 1827. *Neckera tetragona* (Hedw.) Müll. Hal., Syn. Musc. Frond. 2: 125. 1850. *Meteorium tetragonum* (Hedw.) Mitt., J. Linn. Soc., Bot. 12: 431. 1869. *Pilotrichella tetragona* (Hedw.) Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 222. 1872. *Orthostichidium tetragonum* (Hedw.) Müll. Hal., Bull. Herb. Boissier 5: 205. 1897. *Hildebrantiella tetragona* (Hedw.) Paris, Index Bryol. Suppl. 182. 1900. Protologue. E Jamaica asportavit *O. Swartz.*

Plants medium-sized to robust, in pale green to yellow red, loose or dense wefts, often pendent. Primary stems creeping with erect to imbricate leaves, to 60 cm long; rhizoids red brown, smooth or lightly roughened, not or irregularly branched, from clusters of initials at abaxial side of mainly primary stem leaf insertions, but also on abaxial side of leaves on transformed secondary stem and branch tips, and occasionally at base of secondary stems; leaves not spirally arranged, erect, oblong-ovate, 2–3 mm long, hair-pointed, concave, decurrent; margins serrulate throughout, plane to lightly incurved; costae variable, at times absent or short and double, but usually single and ending above midleaf; leaf cells linear to linear-flexuose, smooth, firm- or thick-walled, porose, to 80 × 3 μm, reddish yellow across the base; alar cells quadrate to oblate, thick-walled, in 15–30 rows along the basal margin. Secondary stems irregularly spaced, erect or pendent, not stipitate, sparsely and irregularly branched, stems and branches often transformed to stoloniferous stems at the tips; stems in cross section with sclerodermis of 4–6 rows of small, reddish yellow, thick-walled cells, cortical cells enlarged, yellowish to hyaline, firm- to thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous; stem and branch leaves strongly ranked in seriate rows, erect, oblong-lanceolate to ovate-lanceolate, 1.5–2.0 mm long, cuspidate, occasionally aristate, concave, plicate, decurrent; margins serrulate throughout, incurved near apex or nearly throughout; costae single, mostly reaching 3/4 the leaf length, at times weakly developed, in cross section with 2 layers of thick-walled cells, ventral layer enlarged; leaf cells smooth, thick-walled, porose, apical leaf cells rhomboidal to fusiform, 14–30 × 4–5 μm, median leaf cells linear to linear-flexuose, 30–60 × 3–5 μm; alar cells quadrate to oblate, thick-walled, in 15–30 rows along the basal margin. Dioicous. Perigonia and perichaetia lateral on secondary stems and branches. Perichaetia 4–5 mm long, perichaetial leaves narrowly lanceolate to 4 mm long; vaginulae densely hairy. Setae short, 0.5–0.8 mm long, smooth. Capsules immersed, erect, symmetric, oval to oblong-cylindric, 1.5–2.5 mm long; exothecial cells at mouth thick-walled, quadrate to oblate in 4–6 rows, lower cells irregularly rectangular, firm-walled; stomata absent; opercula conic-rostrate, 0.75–1.0 mm long; annuli rudimentary, of 2–3 rows of quadrate cells mostly clinging to the operculum on dehiscence; peristome diplolepideous; exostome teeth inserted below mouth, narrowly triangular, yellow to orange, smooth, prostome well developed; endostome rudimentary, reduced to hyaline membrane. Spores ovoid to oblong, lightly roughened, 40–70 μm long. Calyptrae cucullate, crispate-pilose, 2.0 mm long.

Illustrations. Hedwig (1801, Pl. 63 1–3); Bartram (1949, Fig. 114 A–C); Arzeni (1954, Pl. 7); Florschütz (1964, Fig. 98); Sharp *et al.* (1994, Fig. 527); Churchill and Linares (1995, Fig. 167 e–g); Duarte Bello (1997, Pl. 186); Buck (1998, Pl. 58 1–6); Gradstein *et al.* (2001, Fig. 195 F–J); Buck (2003, Fig. 114). Figure 67.

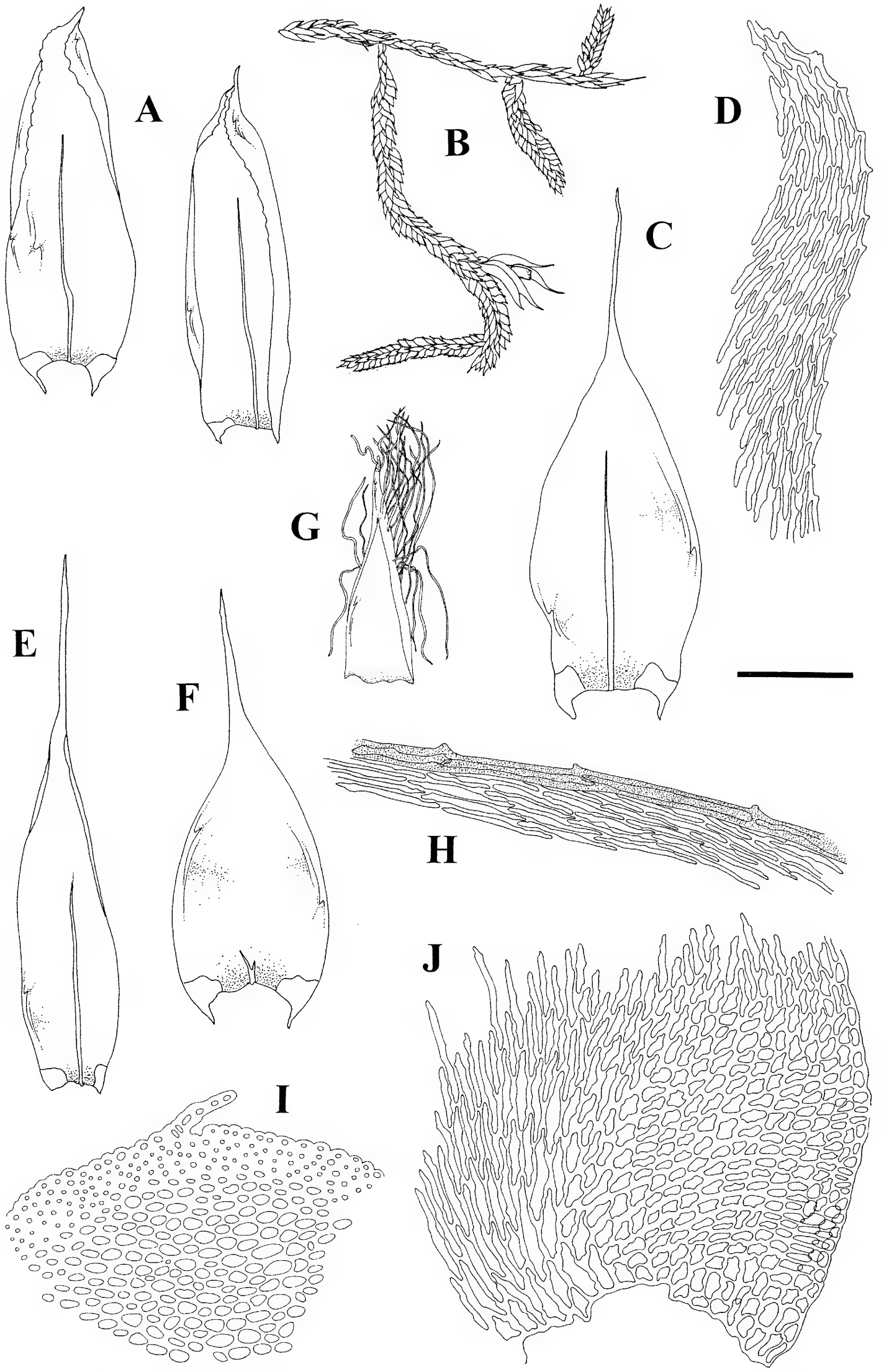


Figure 67. *Orthostichopsis tetragona*. A. Secondary stem and branch leaves. B. Habit. C & F. Primary stem leaves. D. Median leaf cells and margin. E. Stolon leaf. G. Calyptra. H. Upper part of the costa in surface view. I. Stem in cross section. J. Basal and alar cells. Scale in mm: bar = 0.06 (D, H, J); bar = 0.08 (I); bar = 0.5 (A, C, E, F); bar = 0.8 (G); bar = 6.4 (B). All figure parts from *Whittemore 5515*.

Habitat. Pendent on tree trunks, branches, and twigs or vines, on rotting logs, often fallen from canopy branches, occasionally on rocks along rivers; 10–900(1700–2190) m.

Distribution in Central America. BELIZE. Belize: *Allen 17983* (BRH, MO); Cayo: *Allen 18403* (BRH, MO); Corozal: *Davidse & Brant 32515* (BRH, F, MO, NY, US); Orange Walk: *Croat 24991A* (MO); Stann Creek: *Gentle 3048* (F, FH, US); Toledo: *Allen 19052* (BRH, MO). GUATEMALA. Alta Verapaz: *Steyermark 45651* (F, FH, MO); Chiquimula: *Watson 64* (FH); Izabal: *Steyermark 38899* (F, FH, NY); Petén: *Bartlett 12442* (FH, MO, NY, US). HONDURAS. Atlántida: *Hawkins 807* (MO); Isla de la Bahía: *Gaumer 167* (F, FH, NY). NICARAGUA. Boaco: *Stevens 14630* (FH, HNMN, MO); Chontales: *Standley 9005* (F); Granada: *Baker 2526* (FH, MO, NY, US); Managua: *Standley 8196* (F, FH); Río San Juan: *Seymour 6202* (MO); Rivas: *Granzow de la Cerda GC-1649* (DUKE, MO); Zelaya: *Stevens 5085* (DUKE, HNMN, F, FH, MO, NY, US). COSTA RICA. Alajuela: *Standley 40162* (FH, NY, US); Cartago: *Liesner et al. 15268* (MO); Guanacaste: *Standley & Valerio 46380* (FH, NY, US); Heredia: *Opler 1700b* (MO); Limón: *Standley 48688* (FH, NY, US); Puntarenas: *Crosby 3716* (MO); San José: *Dodge & Goerger 9779* (MO). PANAMA. Bocas del Toro: *Allen 5330* (MO); Canal Area: *Crosby 10858* (DUKE, F, FH, MO, NY, PMA, US); Chiriquí: *Hammel 1557* (MO); Coclé: *McPherson 7972* (MO); Colón: *Croat 33642C* (MO, NY, PMA); Darién: *Allen 8771* (MO); Herrera: *McPherson 10271* (MO); Los Santos: *Troll* [*Musci Selecti et Critici 36*] (F, FH, MO, NY, US); Panamá: *Crosby 10895* (DUKE, F, FH, MO, NY, PMA, US), San José Island, *Johnston s.n.* (F, FH, NY); San Blas: *McPherson 11061C* (MO); Veraguas: *Antonio 2274* (MO).

World range: Mexico; Central America; Caribbean; Western and Northern South America, Brazil.

Orthostichopsis tetragona is a common lowland epiphyte in Central America. Although the species occasionally occurs above 1000 meters in Panama, most collections are found between sea level and 200 meters. The leaves of *O. tetragona* are strongly dimorphic. The primary stem leaves are unranked, smooth, and long hair-pointed, while the secondary stem and branch leaves are strongly spirally ranked (whether wet or dry), plicate, and cuspidate. However, leaf form in this species is incredibly plastic, with the stems and branches capable of changing back and forth between one leaf form and the other. Regardless of its variable leaf forms, all collections of *O. tetragona* have at least some typical secondary stem and branch leaves. These stiffly erect, plicate, strongly spirally ranked, cuspidate leaves distinguish it from all other members of *Orthostichopsis*, and they enable the species to be recognized with a hand lens. All other Central American species of *Orthostichopsis* have smooth, hair-pointed secondary stem and branch leaves. The secondary stems are generally weakly branched. They, however, have numerous branch primordia and occasionally the plants are irregularly pinnately branched. Microscopically, *O. tetragona* has extensively developed quadrate to oblate alar cells that extend in 15–30 rows along the basal margins and also nearly reach the costa. The leaf margins are serrulate throughout, and the costa, which is usually two-thirds the leaf length, has odd teeth-like papillae on the dorsal surface.

All other Central American species of *Orthostichopsis* differ from *O. tetragona* in having long-cuspidate to hair-pointed, concave, non-plicate branch leaves and weakly developed (no more than 2–8 rows along the basal margins) alar cells.

Orthostichidium quadrangulare is somewhat similar to *Orthostichopsis tetragona* in size, and its broadly acute leaves are spirally ranked. Plants of *Orthostichidium quadrangulare*, however, are consistently irregularly pinnately branched and the leaves are obscurely ranked when dry. Microscopically, it differs from *Orthostichopsis tetragona* in having mostly ecostate leaves with weakly developed alar cells.

6. *Pireella* Cardot, Rev. Bryol. 40: 17. 1913.

Pirea Cardot *in* Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32(1): 175. 1893 [1894], illegitimate homonym, not *Pirea* Durand, 1888.

Plants small, medium-sized, or robust, in subfrondose to frondose masses on trees and boulders. Primary stems creeping, with small, erect to imbricate, distantly spaced leaves; rhizoids smooth to lightly roughened, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions and at base of secondary stems. Secondary stems irregularly spaced, erect, stipitate,

frondose, pinnately to bipinnately branched, irregularly branched at times with filiform branches, occasionally unbranched; cross section with sclerodermis, enlarged firm-walled cortical cells, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous. Stipe leaves appressed or squarrose-recurved from a broadly ovate, clasping base, rounded to the insertions or auriculate; margins plane or narrowly recurved. Secondary stem leaves erect-appressed, erect-spreading to spreading, not obviously ranked, lanceolate to ovate-lanceolate or ovate-ligulate, acuminate, concave, at times lightly rugose when dry, not plicate, shortly decurrent. Branch leaves lanceolate, narrowly ovate-lanceolate, ovate-linear, or ovate-ligulate, at times strongly ranked; margins serrulate to denticulate above, serrulate to subentire below, plane above, at times narrowly recurved below; costae percurrent, subpercurrent or ending well below apex; cells smooth or prorate, variably porose, firm- to thick-walled throughout, apical cells fusiform-sigmoid or oval to rounded-rhomboidal, median cells at leaf concavity linear-flexuose or oval to rounded-rhomboidal; alar cells weakly or strongly differentiated, cells across the insertions reddish yellow. Asexual reproduction by uniseriate, septate gemmae arising from circular clusters of initials in leaf axils, or by deciduous branch leaves. Dioicous. Setae short or long, smooth or scabrous. Capsules immersed or exserted, erect, symmetric, oval-oblong, cylindrical, oval to orbicular; stomata absent; opercula conic-apiculate to conic-rostrate; annuli rudimentary; peristome diplolepideous, exostome deeply inserted within capsule mouth, teeth 16 or at times united into 8 pairs, prostome well developed; endostome rudimentary. Calyptrae cucullate or mitrate, variously hairy.

Pireella is a genus of 13 species (11 in Central America) restricted to the Western Hemisphere. The genus is characterized by erect, stipitate secondary stems that are irregularly spaced on creeping primary stems. The secondary stems are frequently pinnately or bipinnately branched. The branch leaves in *Pireella* are often spirally ranked, at times lightly rugose, broadly ovate to lanceolate, and usually concave. A majority of the species have percurrent to subpercurrent costae, but in a few species they end well below the apex. The leaf cells in *Pireella* are firm-walled throughout, variously porose and either smooth or prorate. The upper and median cells vary from oval to elongate-sigmoid, and this is an important taxonomic feature of the genus. Alar cell development is extremely variable amongst the species of *Pireella*. Some species have nearly undifferentiated alar cells, while in others they are as well developed as those of *Cryphaea*.

Pireella is a dioicous genus, and sporophytes are not often encountered. The genus, however, often reproduces asexually by means of axillary gemmae or deciduous branch leaves. The setae of *Pireella* can be long or short, and smooth or scabrous, while the capsules vary from orbicular to cylindrical in shape. Its diplolepideous peristome is irregularly formed, with a well-developed prostome and greatly reduced to nearly absent endostome. The calyptrae are variously hairy, and they can be either large and cucullate or small and mitrate. Arzeni (1954) treated the genus *Pireella* in Central America. The West Indian treatment of *Pireella* by Buck (1998) treats seven of the eleven Central American species of the genus. *Pireella* was revised by Newton (1993) in an unpublished Ph.D. dissertation.

The name *Pireella* was given by Jules Cardot in honor of his father-in-law, the Belgian botanist, Louis Alexandre Henri Joseph Piré (3 March 1827–16 July 1887).

1. Stipe leaves recurved to squarrose 2
1. Stipe leaves erect or appressed 5

2. Costa of branch leaves reaching 2/3 the leaf length . . . . . 7. *P. hondurensis*
2. Costa percurrent to subpercurrent 3

3. Branch leaves long-lanceolate, often deciduous . . . . . 1. *P. angustifolia*
3. Branch leaves ovate-lanceolate, not deciduous. 4

4. Stipe and stem leaves rounded to insertion; capsules immersed . . . . . 5. *P. filicina*
4. Stipe and stem leaves strongly auriculate; capsules exserted . . . . . 6. *P. guatemalensis*

5. Branch leaf costae reaching 2/3 the leaf length . . . . . 4. *P. falcifolia*
5. Branch leaf costae percurrent to subpercurrent 6

6. Branch leaf cells above midleaf at middle of leaf concavity ovoid, usually smooth, 5–16 μm long 7
6. Branch leaf cells above midleaf at middle of leaf concavity elongate-sigmoid, usually strongly prorate, 16–30 μm long 9

7. Secondary stem leaves twice as large as branch leaves; branch leaf alar cells hardly differentiated; capsules ovoid to subglobose . . . . . 8. *P. mariae*
7. Secondary stem and branch leaves similar in size; branch leaf alar cells differentiated in numerous rows of quadrate cells; capsules long-cylindrical 8

8. Leaves rugose; secondary stem leaf margins tightly recurved in places; asexual gemmae on leaf tips . . . . . 2. *P. crosbyi*
8. Leaves not rugose; secondary stem leaf margins plane or erect; asexual gemmae in leaf axils . . . . . 11. *P. pycnothallodes*

9. Secondary stems not or weakly branched; alar cells quadrate, in numerous rows extending 6–10 cells up the margins . . . . . 3. *P. cymbifolia*
9. Secondary stem leaves densely branched; alar cells weakly developed, extending 1–4 cells up the margins 10

10. Plants 1.5–3.0 cm long; stipe leaf margins narrowly recurved . . . . . 9. *P. papillosula*
10. Plants 2–10 cm long; stipe leaf margins plane . . . . . 10. *P. pohlii*

1. *Pireella angustifolia* (Müll. Hal.) Arzeni, Amer. Midl. Naturalist 52: 29. 1954. *Pilotrichum angustifolium* Müll. Hal., Syn. Musc. Frond. 2: 181. 1851. *Pterobryon angustifolium* (Müll. Hal.) Mitt., J. Linn. Soc., Bot. 12: 426. 1869. Protologue. Insula Trinidad Antillarum, ubi in monte Tocuche, 3400 ped. alto, 1847 *Crüger* legit.

Pterobryon angustifolium fo. *flagelliferum* Besch., Ann. Sci. Nat., Bot. sér. 6, 3: 223. 1876. *Pterobryon angustifolium* var. *flagelliferum* (Besch.) Besch., J. Bot. (Morot) 8: 62. 1894. Protologue. Guadeloupe, sur les arbres pourris au bord de la rivière du Galéon et des Bains jaunes, 1100 m altit. (*Beaupertuis*, 1839, in herb. Mus. Paris, stérile).

Pterobryon integrifolium Hampe *ex* Besch., J. Bot. (Morot) 8: 62. 1894. Protologue. Guadeloupe, à la base des arbres, bord de la rivière du Galéon, aux Bains jaunes, alt. 1100 m (*Beaupertuis*, 1839, in herb. Mus. Paris).

Pterobryon angustifolium var. *flabelliforme* Besch. *ex* Arzeni, Amer. Midl. Naturalist 52: 29. 1954, invalid name, listed in synonymy.

Plants medium-sized to robust, in dark green or yellow green, thin or dense, dendroid masses on trees and boulders. Primary stems creeping, with small, erect to imbricate, distantly spaced leaves; rhizoids dark red, smooth to lightly roughened, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions and at base of secondary stems. Secondary stems irregularly spaced, erect, stipitate, frondose to regularly pinnately branched, 3–10 cm long, at times with filiform branches; stems in cross section with sclerodermis of 6–8 rows of small, red, very thick-walled cells, cortical cells enlarged, yellow, thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous. Stipe leaves squarrose-recurved from a broadly ovate, clasping base, 1.5–3.0 mm long. Secondary stem leaves erect-spreading to spreading, not obviously ranked, 2–3 mm long, lanceolate to ovate-lanceolate, broadly acuminate, concave, at times lightly rugose when dry, not plicate, shortly decurrent; margins serrulate to denticulate above, serrulate to subentire below, plane above, at times narrowly recurved below; costae single, subpercurrent; cells smooth or prorate, variably porose, firm- to thick–walled throughout, apical cells fusiform-sigmoid, 16–30 × 4–6 μm, median cells linear-flexuose, 40–60 × 4–6 μm; alar cells hardly differentiated, of a few irregularly subquadrate, incrassate, porose cells at the basal angles, cells across the insertions reddish yellow. Branch leaves lanceolate, 1.5–2.5 mm long, otherwise similar to secondary stem leaves. Asexual reproduction commonly by deciduous branch leaves, also by uniseriate, septate gemmae arising from circular clusters of initials in leaf axils. Dioicous. Perigonia lateral on upper secondary stems and branches. Perichaetia large, leaves oblong-lanceolate, 5–6 mm long. Setae short, smooth, reddish, 0.5 mm long. Capsules immersed, erect, symmetric, oval-oblong, 2–3 mm long; exothecial cells at mouth dark red, oblate in

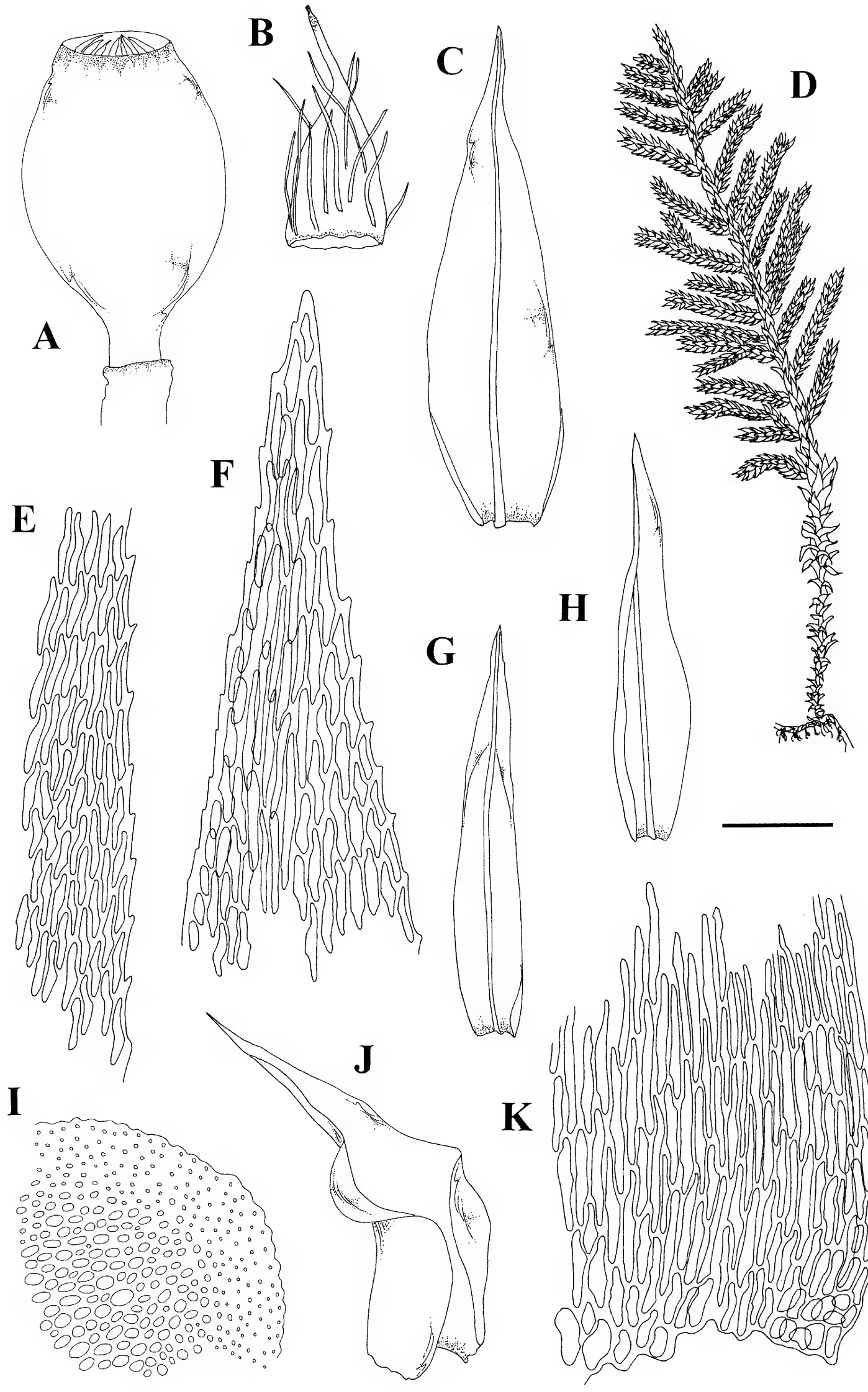
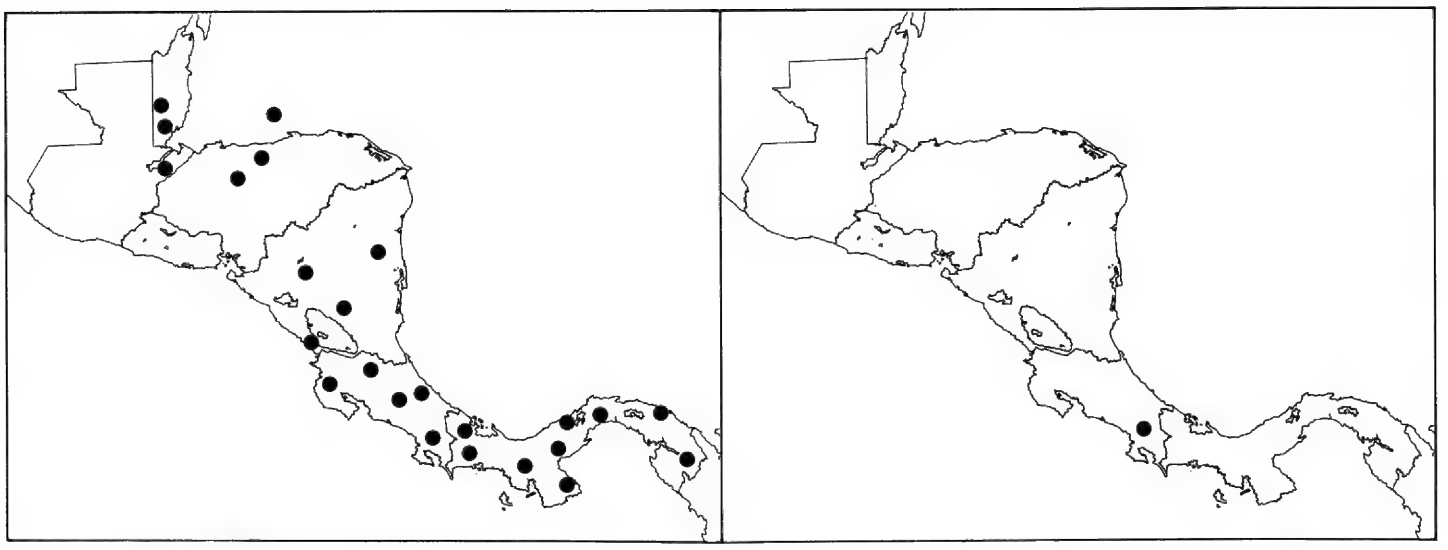


Figure 68. *Pireella angustifolia*. A. Seta and capsule. B. Calyptra. C. Stem leaf. D. Habit. E. Median leaf cells and margin. F. Leaf apex. G & H. Branch leaves. I. Stem in cross section. J. Stipe leaf. K. Basal and alar cells. Scale in mm: 0.05 (E, F, K); bar = 0.5 (B, C, G, H, J); bar = 0.8 (I); bar = 0.9 (A); bar = 8.6 (D). All figure parts from *Allen 15062*.



Pireella angustifolia *Pireella crosbyi*

8–10 rows, lower cells short-rectangular to rounded-quadrate, firm-walled; stomata absent; opercula conic-apiculate to short conic-rostrate, 0.5 mm long; annuli rudimentary; peristome diplolepideous; exostome teeth 16 or at times united into 8 pairs, deeply inserted within capsule mouth, yellow or red, linear-triangular, to 350 μm long, smooth, weakly trabeculate, prostome well developed; endostome rudimentary. Spores round to oblong, smooth to lightly roughened, 30–40 μm. Calyptrae mitrate, 1.0–1.5 mm long, densely hairy.

Illustrations. Bartram (1949, Fig. 117 A–C); Arzeni (1954, Pl. 18 1–10); Duarte Bello (1997, Pl. 187); Buck (1998, Pl. 52 1–8). Figure 68.

Habitat. On bark of tree trunks, branches, twigs, logs, vines, and occasionally on boulders; 75–1676 m.

Distribution in Central America. BELIZE. Cayo: *Allen 18379* (BRH, MO); Toledo: *Allen 19005* (BRH, MO). GUATEMALA. Izabal: *Steyermark 38892* (F, FH). HONDURAS. Atlántida: *Allen 17248* (MO, TEFH); Isla de la Bahía: *Gaumer* (F, FH, NY); Yoro: *Allen 13629* (MO). NICARAGUA. Chontales: *Standley 9089* (F, FH); Matagalpa: *Stevens 9651a* (MO); Rivas: *Granzow de la Cerda GC-1647* (DUKE, MO); Zelaya: *Stevens 8388A* (MO). COSTA RICA. Alajuela: *Liesner 5084* (CR, MO); Cartago: *Nebel* (US); Guanacaste: *Standley & Valerio 46404* (FH, NY, US); Limón: *Herrera 2236* (CR, MO, NY); Puntarenas: *Crosby 3712* (MO). PANAMA. Bocas del Toro: *Allen 5791* (MO); Chiriquí: *Valentine* (NY); Coclé: *McPherson 7972D* (MO); Colón: *Crosby 10346* (MO, PMA); Darién: *Allen 8917A* (MO); Los Santos: *Croat 34542B* (MO); Panamá: *Crosby 4452* (F, MO, NY, US); San Blas: *D'Arcy 13672B* (MO); Veraguas: *Hammel 4720* (MO).

World range: Mexico; Central America; Caribbean; Western and Northern South America.

Pireella angustifolia is one of the largest species of *Pireella*. It is a commonly encountered species in Central America, where the plants often have sporophytes. In addition to its large size, the species is distinguished by its squarrose-recurved stipe leaves and long, lanceolate branch leaves that are often readily deciduous. The branch leaf cells in *P. angustifolia* are elongate; however, they are also extremely variable in size. Newton (1993), for example, found that individual upper leaf cell lengths can vary from 10–39 μm. Sporophytically, the species is marked by its oval-oblong, immersed capsules and its short, mitrate calyptra.

Pireella filicina and *P. guatemalensis* are similar to *P. angustifolia* in having squarrose-recurved stipe leaves. *Pireella filicina* and *P. angustifolia* also have oval-oblong capsules and short, mitrate calyptrae. *Pireella filicina* differs from *P. angustifolia* in having ovate acuminate branch leaves that are never deciduous and shorter (cell length: width 1–3:1 vs. 4–7: 1) upper leaf cells. *Pireella guatemalensis* differs from *P. angustifolia* in having strongly auriculate stipe leaves, ovate branch leaves that are not deciduous, long-exserted, cylindric capsules, and large, cucullate calyptrae.

Mitten (1869) treated *Pireella angustifolia* and *Pterobryon densum* together in the section *Eupterobryum*, and Brotherus (1925) also placed *Pireella angustifolia* in *Pterobryon*. These species in-

tegrate in plant size and share the features of immersed, oval-oblong capsules; short, mitrate calyptrae; and nearly undifferentiated alar cells. Arzeni (1954) transferred *Pterobryon angustifolium* to *Pireella* on the basis of its flagelliform branches and 5-seriate, lanceolate branch leaves with often prorate leaf cells. However, both *Pterobryon densum* and *Pireella angustifolia* have lanceolate branch leaves, and in Central America *Pireella angustifolia* does not have ranked branch leaves. *Pterobryon densum* also differs from *Pireella angustifolia* in having appressed stipe leaves and strongly plicate secondary stem and branch leaves. There are, however, numerous *Pireella* species with appressed stipe leaves. Buck (1998) questioned whether *Pireella* was distinct from *Pterobryon*; the two genera appear to differ only in the plicate leaves of *Pterobryon*.

2. *Pireella crosbyi* B. H. Allen, *sp. nov.* Type. Costa Rica. Puntarenas: Hills on N side of Pan-American Highway, ca. 4 miles N of Palmar Sur, *Crosby 3831* (MO, holotype).

Species haec *Pireellae pycnothallodi* simili sed foliis rugosis, marginibus foliorum caulium secundariorum anguste recurvis et gemmis apicibus foliorum differt.

Plants small to medium-sized, in yellow green, thin, frondose masses. Primary stems creeping, with small, imbricate, distantly spaced leaves; rhizoids dark red, smooth to lightly roughened, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions and at base of secondary stems. Secondary stems irregularly spaced, erect, stipitate, pinnately branched, to 3 cm long; stems in cross section with sclerodermis of 6–8 rows of small, red to orange brown, very thick-walled cells, cortical cells enlarged, hyaline to yellowish, firm- to thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous. Stipe leaves erect to appressed, broadly triangular-ovate, 1–1.5 mm long, rounded at base, decurrent, acuminate; margins subentire to lightly serrulate, often tightly recurved; costae percurrent to subpercurrent; alar cells quadrate in numerous rows. Secondary stem leaves erect, not obviously ranked, 1.6–1.8 mm long, broadly ovate-lanceolate, more or less clasping, gradually acuminate, concave, rugose, rounded to the insertions, decurrent; margins entire to lightly serrulate, often narrowly and tightly recurved in places, otherwise plane; costae single, percurrent to shortly excurrent, often wavy above, more or less expanded in the apex; alar cells quadrate in numerous rows. Branch leaves erect-incurved when dry, erect-spreading when wet, weakly ranked, ovate-lanceolate, 1.2–1.4 mm long, broadly or narrowly acuminate, concave, rugose, somewhat rounded to the insertions, decurrent; margins entire to lightly serrulate above, erect to plane; costae single percurrent to subpercurrent, more or less expanding in the apex; cells smooth, firm-walled throughout, apical cells oval to rounded-rhomboidal, occasionally elongate, 8–20 × 4–6 μm, median cells in concave part of leaf oval to rounded-rhomboidal, occasionally elongate, 8–15 × 4–6 μm; alar cells quadrate in numerous rows, cells across the insertions porose, reddish yellow. Asexual reproduction by uniseriate, septate gemmae arising from initials on leaf apices. Dioicous (?). Sporophytes unknown.

Illustration. Figure 69.
Habitat. Epiphytic.
Distribution in Central America. COSTA RICA. Puntarenas: *Crosby 3831* (MO).
World range: Central America.

Pireella crosbyi is a small to medium-sized species with regularly branched stems and erect to appressed stipe leaves. The stipe and the secondary stem leaf margins of *P. crosbyi* are in part narrowly and tightly recurved. A distinctive feature of *P. crosbyi* is the presence of rugose, ovate-lanceolate secondary stem and branch leaves that are more or less similar in size. The median branch leaf cells in the upper region of the leaf concavity of *P. crosbyi* vary considerably in shape, but are mainly ovate and firm- to thick-walled. The cells in the secondary stem and branch leaf apices of *P. crosbyi* are more or less elongate. However, at the extreme apex the cells are often differentiated into nematogen cells that give rise to asexual gemmae. An important feature of *P. crosbyi* is the presence of the numerous rows of quadrate cells in the alar regions of the stipe, secondary stem, and branch leaves.

Pireella pycnothallodes is very similar to *P. crosbyi*; both species have erect-appressed stipe leaves, short, oval to rhomboidal cells in the median region of the leaf concavity, and alar cells

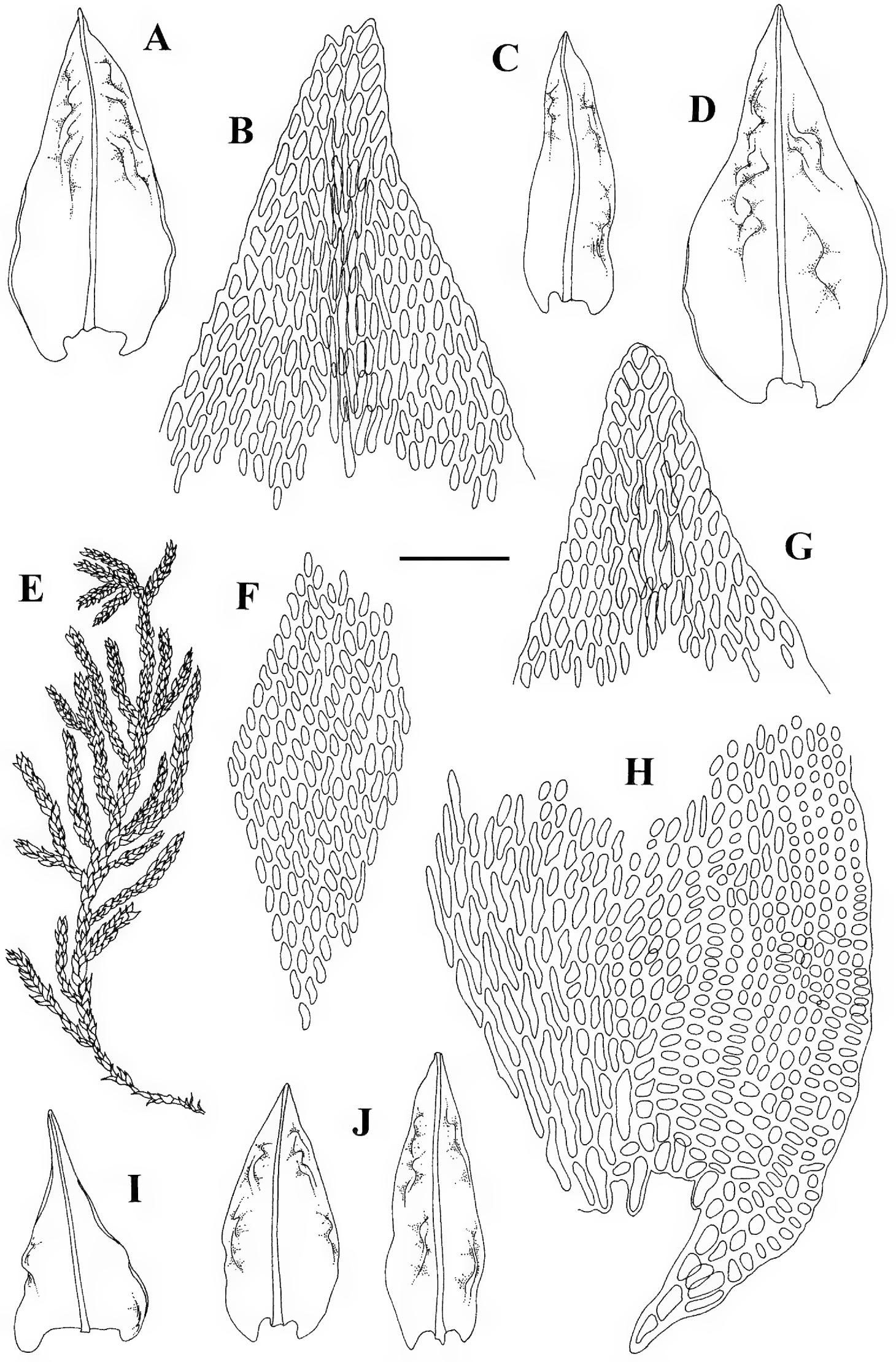


Figure 69. *Pireella crosbyi*. A & D. Stem leaves. B & G. Branch leaf apices. C & J. Branch leaves. E. Habit. F. Median leaf cells. H. Basal and alar cells. I. Stipe leaf. Scale in mm: bar = 0.05 (B, F–H); bar = 0.5 (A, C, D, I, J); bar = 5.1 (E). All figure parts from *Crosby 3831* (type).

strongly differentiated into numerous rows of quadrate cells. It differs from *P. crosbyi* in having non-rugose leaves, secondary stem leaves with plane or erect margins, and gemmae that are axillary on the stems rather than arising from the leaf apices. *Pireella cymbifolia* and *P. crosbyi* also have erect-appressed stipe leaves and leaves with numerous rows of quadrate alar cells. *Pireella cymbifolia* differs from *P. crosbyi* in having non-rugose leaves, weakly branched stems, elongate, sinuose cells in the median region of the leaf concavity, and gemmae that are axillary on stems. There could be some confusion between *P. mariae* and *P. crosbyi*, because both species have erect-appressed stipe leaves and short, oval to rhomboidal cells in the median region of the leaf concavity. *Pireella mariae* differs from *P. crosbyi* having stem leaves that are twice as large as the branch leaves and weakly to hardly differentiated alar cells. *Pireella filicina* is similar to *P. crosbyi* in having short branch leaf cells. It differs from *P. crosbyi* in having squarrose stipe leaves, non-rugose leaves, and alar cells not or hardly differentiated. *Pireella pergemmescens* H. Rob. is the only other *Pireella* species with nematogen cells in the leaf apices that give rise to asexual gemmae. It differs from *P. crosbyi* in having non-rugose leaves with more elongate upper leaf cells, and considerably fewer quadrate cells in the alar regions.

3. *Pireella cymbifolia* (Sull.) Cardot, Rev. Bryol. 40: 17. 1913. *Pilotrichum cymbifolium* Sull. *in* A. Gray, Manual (ed. 2), 681. 1856. *Pterobryon cymbifolium* (Sull.) Mitt., J. Linn. Soc., Bot. 12: 426. 1869. *Neckera cymbifolia* (Sull.) Müll. Hal., Flora 58: 92. 1875. *Pilotrichella cymbifolia* (Sull.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 254. 1877. *Pirea cymbifolia* (Sull.) Broth., Nat. Pflanzenfam. I(3): 796. 1906. Protologue. [United States] From a tree on a hummock, E. Florida, *ex herb. Gray*.

Pireella denticulata Cardot & Thér. *in* Cardot, Rev. Bryol. 40: 17. 1913, invalid name, lacks a description.
Pireella denticulata Cardot & Ther. *in* Thér., Mem. Soc. Cub. Hist. Nat. "Felipe Poey" 14: 359. 1940. Protologue. [Cuba] Sierras de Banao (*Léon 2727 p.p.*).

Plants small to medium-sized, in light green or yellow green, thin or dense, subfrondose masses. Primary stems creeping, with small, erect to imbricate, distantly spaced leaves; rhizoids dark red, smooth to lightly roughened, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions and at base of secondary stems. Secondary stems 2–7 cm long, irregularly spaced, erect, stipitate, unbranched, sparsely branched, or rarely irregularly subpinnately branched, often with flagellate branches; stems in cross section with sclerodermis of 3–5 rows of small, red to orange brown, very thick-walled cells, cortical cells enlarged, hyaline to yellowish, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous. Stipe leaves erect to erect-appressed, ovate-triangular, 0.8–1.2 mm long, not rounded at base, decurrent, acuminate; margins denticulate; costae percurrent to subpercurrent; alar cells quadrate in numerous rows. Secondary stem leaves erect, lightly ranked, 1.5–2.0 mm long, ovate-lanceolate, clasping at base, gradually acuminate, strongly concave, not plicate, not rounded to the insertions, decurrent; margins serrate to subdenticulate, plane; costae single, subpercurrent to percurrent, often wavy above; alar cells quadrate in numerous rows. Branch leaves erect to erect-spreading, distinctly ranked when wet, ovate to ovate-lanceolate, 1.0–1.5 mm long, broadly acuminate, strongly concave, not plicate, not rounded to the insertions, decurrent; margins serrulate to serrate, erect to plane; costae single, percurrent to subpercurrent; cells prorate, thin- or firm-walled throughout, occasionally porose, apical cells elongate-sigmoid, 18–30 × 4–6 μm, median cells in concave part of leaf elongate-sigmoid, 16–30 × 4–6 μm; alar cells quadrate in numerous rows, cells across the insertions often porose, reddish yellow. Asexual reproduction by uniseriate, septate gemmae arising from circular clusters of initials in leaf axils; germinated cells smaller and densely papillose. Dioicous. Perigonia lateral on upper secondary stems and branches, 1 mm long. Perichaetial leaves ovate-lanceolate, 1.5–2.5 mm long, abruptly long-acuminate, inner leaves setaceous; vaginulae hairy. Setae elongate, smooth, yellow, orange brown with age, 6–11 mm long. Capsules exserted, erect, symmetric, cylindrical, 2.0–2.5 mm long; exothecial cells at mouth red, rounded-quadrate to oblate in 8–10 rows, lower cells rounded, short-rectangular, firm- to thick-walled; stomata absent; opercula conic-rostrate, 1.0 mm long; annuli simple, of 2–4 rows of firm-walled, quadrate cells; columella brownish, 2.0 × 0.4 mm; peristome diplolepideous; exostome teeth 16, inserted within capsule mouth, pale reddish yellow, irregularly developed, linear-triangular, to 200 μm long,

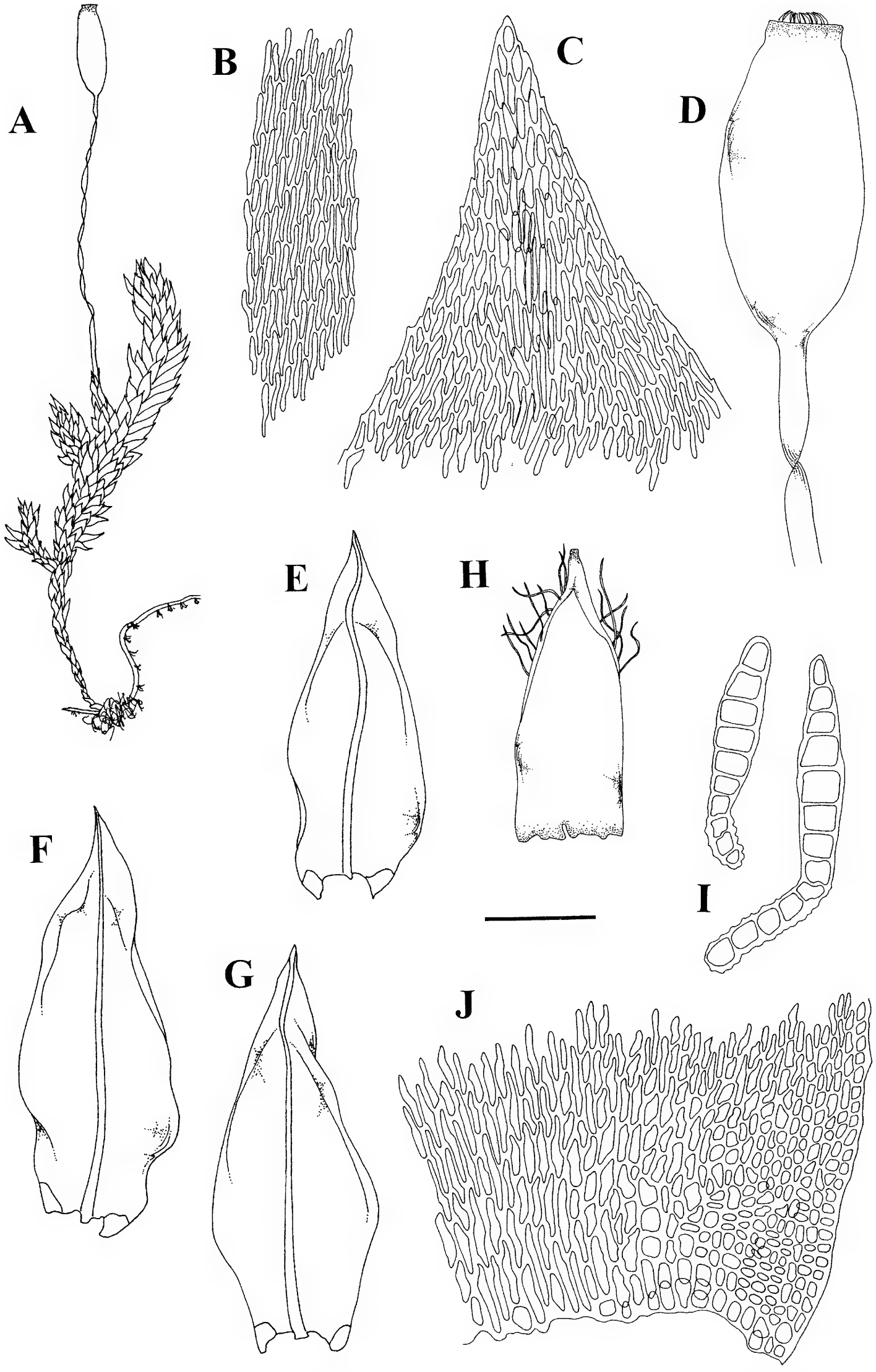
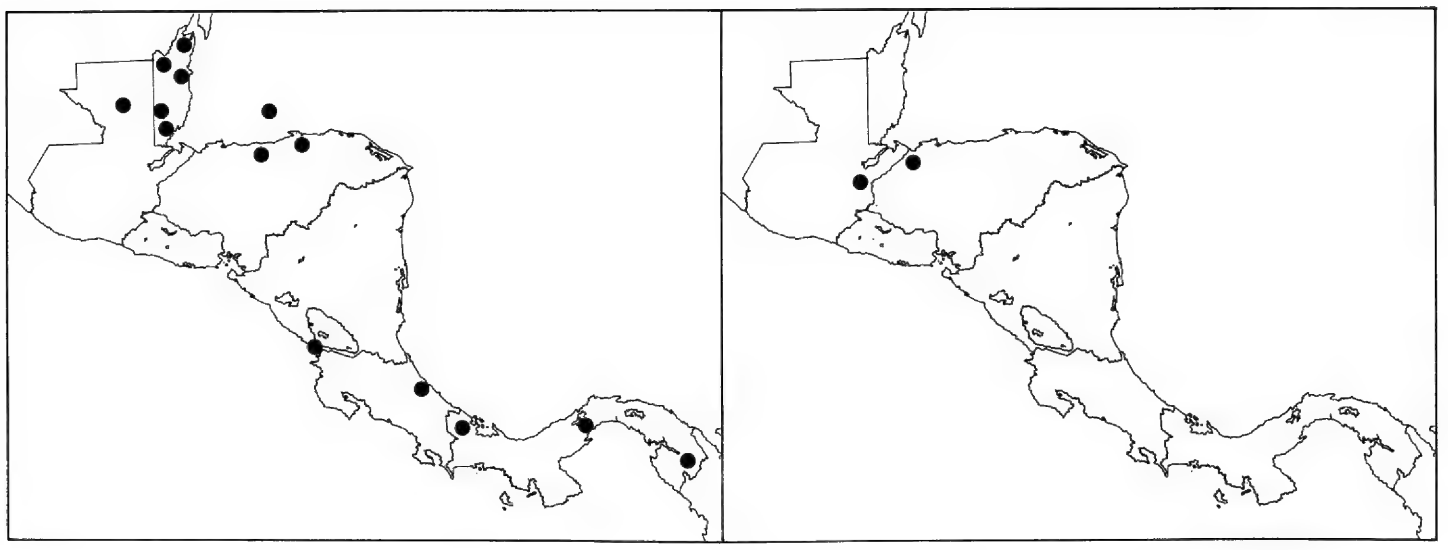


Figure 70. *Pireella cymbifolia*. A. Habit. B. Median leaf cells. C. Leaf apex. D. Seta and capsule. E–G. Secondary stem leaves. H. Calyptra. I. Gemmae. J. Basal and alar cells. Scale in mm: bar = 0.06 (B, C, I, J); bar = 0.4 (E–G); bar = 0.9 (D, H); bar = 3.3 (A). A, D, E–H from *Allen 17181*; all other figure parts from *Allen 18195*.



Pireella cymbifolia *Pireella falcifolia*

smooth, weakly trabeculate, prostome well developed; endostome rudimentary. Spores irregularly rounded to oblong, lightly roughened, 30–36 μm. Calyptra cucullate, hairy, 2.5 mm long.

Illustrations. Sullivant (1864, Pl. 76 B); Grout (1934, Pl. 56 B); Thériot (1940, Pl. 54 7); Arzeni (1954, Pls. 25–27); Breen (1963, Pl. 109 5–10); Crum and Anderson (1981, Fig. 383 A–E); Sharp *et al.* (1994, Fig. 533); Duarte Bello (1997, Pl. 189); Buck (1998, Pl. 55 8–13); Buck (2003, Fig. 115 H–M). Figure 70.

Habitat. On tree trunks, vines, and rotting logs; 7–520 m.

Distribution in Central America. BELIZE. Belize: *Gentle 1659* (F, FH); Cayo: *Allen 18195* (BRH, MO); Corozal: *Davidse & Brant 32554* (MO); Orange Walk: *Mann 43* (NY); Toledo: *Gentle 4931* (MO). GUATEMALA. Petén: *Lundell 2037* (FH, US). HONDURAS. Atlántida: *Allen 17181* (MO, TEFH); Colón: *Saunders 833* (MO); Isla de la Bahía: *Gaumer 1213a* (NY). NICARAGUA. Rivas: *Granzow de la Cerda GC-1640a* (DUKE, MO). COSTA RICA. Limón: *Steere CR-118* (NY). PANAMA. Bocas del Toro: *Crosby 4085* (MO); Canal Area: *Salazar & Correa 1327* (MO); Darién: *Allen 8705* (MO).

World range: Southeastern U.S.A.; Mexico, Central America; Caribbean; Northern and Western South America.

Pireella cymbifolia is a small to medium-sized species with erect to erect-appressed stipe leaves and typically weakly branched or unbranched secondary stems. The secondary stem leaves and branch leaves of *P. cymbifolia* are ovate-lanceolate, more or less equal-sized, and not rounded to the insertions. The leaf cells in the upper median region of the leaf concavity are elongate-sigmoid and commonly prorate, while the alar cells are quadrate to subquadrate in numerous rows. *Pireella cymbifolia* has elongate setae, cylindrical capsules, and large, hairy, cucullate calyptrae.

Pireella pycnothallodes is similar to *P. cymbifolia* in having erect stipe leaves, numerous quadrate alar cells in all its leaves, elongate setae, cylindrical capsules, and large, cucullate calyptrae. Its stems, however, are pinnately to bipinnately branched, and the cells in the upper, median region of the leaf concavity are short and oval. *Pireella pohlii* has often been confused with *P. cymbifolia*, because both species have erect stipe leaves, elongate-sigmoid cells in the upper, median region of the leaf concavity, elongate setae, cylindrical capsules, and large, cucullate calyptrae. It differs from *P. cymbifolia* in having pinnately branched stems, stem and stipe leaves that are rounded to auriculate at base, and poorly developed alar cells that consist of only a few quadrate cells. *Pireella papillosula* has stipe leaves with recurved margins and differs from *P. cymbifolia* in its much smaller size and regularly bipinnately branched secondary stems.

4. *Pireella falcifolia* E. B. Bartram, Bryologist 49: 117. 1946. Protologue. Guatemala. Dept. Zacapa: cloud forest in ravine bordering Quebrada Alejandria, summit of Sierra de las Minas, vicinity of Finca Alejandria, alt. 2500 m, *Steyermark 29868*. Types. Guatemala. Dept. Zacapa: cloud forest

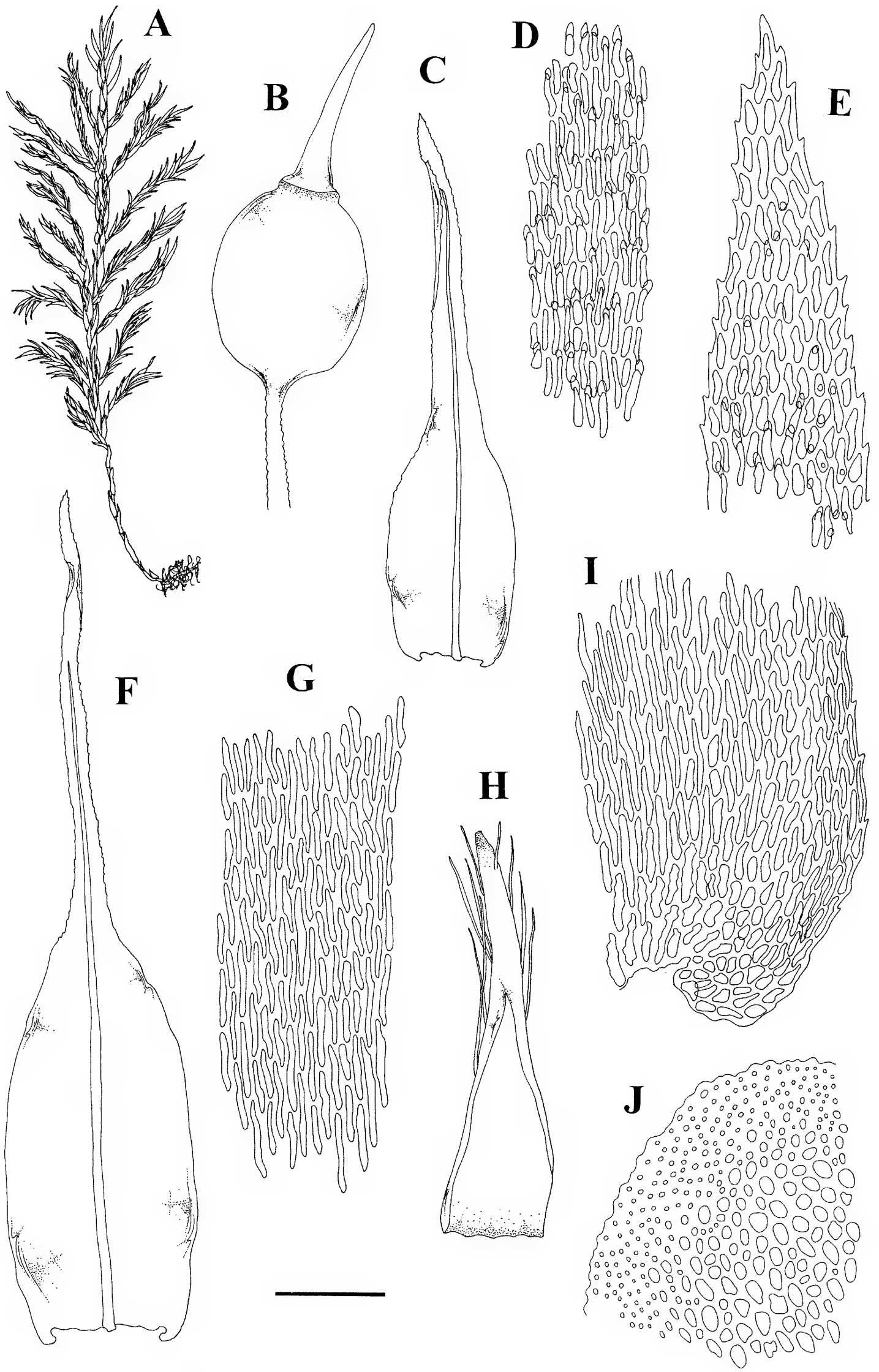


Figure 71. *Pireella falcifolia*. A. Habit. B. Seta, capsule, and operculum. C. Branch leaf. D. Upper leaf cells. E. Leaf apex. F. Stem leaf. G. Median leaf cells. H. Calyptra. I. Basal and alar cells. J. Stem in cross section. Scale in mm: bar = 0.06 (D, E, G, I); bar = 0.08 (J); bar = 0.6 (C, F); bar = 0.9 (B, H); bar = 6.4 (A). All figure parts from *Allen 14156*.

in ravine bordering Quebrada Alejandria, summit of Sierra de las Minas, vicinity of Finca Alejandria, alt. 2500 m, Oct 13, 1939, *J. A. Steyermark 29868* (FH, holotype; F, isotype).

Plants medium-sized to large, in yellow green, thin or dense, frondose masses. Primary stems creeping, with small, erect to imbricate, distantly spaced leaves; rhizoids dark red, smooth to lightly roughened, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions and at base of secondary stems. Secondary stems irregularly spaced, erect, stipitate, densely pinnately or bipinnately branched, 4–10 cm long; stems in cross section with sclerodermis of 6–8 rows of small, red, very thick-walled cells, cortical cells enlarged, yellow, thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous. Stipe leaves appressed, 3.5–5 mm long, from broadly ovate bases abruptly narrowed to long narrowed acumina, rounded to the insertions, shortly decurrent; margins serrate to denticulate above; upper cells strongly prorate. Secondary stem leaves erect, not obviously ranked, 4.0–6.0 mm long, ovate-lanceolate to ovate-ligulate, abruptly narrowed to long narrowed acumina, plane, at times lightly rugose when dry, not plicate, rounded to the insertions, shortly decurrent; margins denticulate above, subentire below, plane; costae single, reaching 2/3 the leaf length; upper cells elongate, strongly prorate. Branch leaves erect-falcate, not ranked, 2.5–3.5 mm long, narrowly ovate-lanceolate, ovate-linear, or ovate-ligulate, abruptly long-acuminate, at times lightly rugose when dry, not plicate, rounded to the insertions, shortly decurrent; margins denticulate to serrate above; costae reaching 2/3 the leaf length; cells firm-walled throughout, upper cells strongly prorate, apical cells fusiform-sigmoid to rounded-rhomboidal, 12–30 × 4–6 μm, median cells fusiform-sigmoid to elongate, 12–30 × 3–5 μm; basal cells 30–60 μm; alar cells weakly differentiated, of a few irregularly subquadrate, incrassate, porose cells at the basal angles, cells across the insertions porose, reddish yellow. Asexual gemmae present in leaf axils. Dioicous. Perigonia lateral on upper secondary stems and branches. Perichaetial leaves lanceolate-ovate, 4 mm long, abruptly narrowed to long awns; vaginulae hairy. Setae long, scabrous above, red, 5–9 mm long. Capsules exserted, erect, symmetric, oval to orbicular, orange red, 1.5–2.0 mm long; exothecial cells at mouth red, rounded-quadrate to oblate in 8–10 rows, lower exothecial cells rounded, short-rectangular, subquadrate to oblate, firm-walled; stomata absent; opercula conic-rostrate, 1.5–2.0 mm long; annuli simple, of 2–4 rows of firm-walled, quadrate cells; columella pale yellow, thick, 1.5 × 0.8 mm; peristome diplolepideous; exostome teeth fused into 8 pairs, deeply inserted within capsule mouth, pale yellow to hyaline, irregularly developed, linear-triangular, to 450 μm long, smooth, weakly trabeculate, prostome well developed; endostome rudimentary. Spores irregularly rounded to ovoid, smooth to lightly roughened, 10–20 μm. Calyptrae cucullate, 2.5–3.0 mm long, sparsely hairy.

Illustrations. Bartram (1949, Fig. 116 A–D); Arzeni (1954, Pl. 14, Pl. 15 13–23). Figure 71.

Habitat. On tree trunks and branches; 1500–2500 m.

Distribution in Central America. GUATEMALA. Zacapa: *Steyermark 29868* (F, FH). HONDURAS. Cortés: *Allen 14156* (MO).

World range: Central America.

Pireella falcifolia is a medium-sized to large species with appressed stipe leaves and long, falcate branch leaves. The leaves of *P. falcifolia* are narrowly ovate-lanceolate, ovate-linear, or ovate-ligulate and abruptly long-acuminate, with costae that end considerably below the apex. The upper leaf cells, although extremely variable in shape in size, are mostly elongate-sigmoid and strongly prorate. The leaves are sharply serrulate to denticulate above, rounded to the insertions, and the alar cells are weakly differentiated. The setae in *P. falcifolia* are long and scabrous above, the capsules orbicular, the operculum conic-rostrate, and the calyptrae are large and cucullate.

Pireella hondurensis is nearly identical in aspect to *P. falcifolia*, and both species have falcate, similarly shaped branch leaves, strongly prorate upper cells, and short costae. Furthermore, these species also have elongate, scabrous setae and orbicular capsules. *Pireella hondurensis* differs from *P. falcifolia* in having deciduous branch leaves and strongly auriculate stipe leaves that are clasping at base but squarrose-recurved above.

5. *Pireella filicina* (Hedw.) Cardot, Rev. Bryol. 40: 18. 1913. *Neckera filicina* Hedw., Sp. Musc. Frond. 204. 1801. *Pterobryon filicinum* (Hedw.) Mitt., J. Linn. Soc., Bot. 12: 425. 1869. *Pirea filicina* (Hedw.) Broth., Nat. Pflanzenfam. I(3): 796. 1906. Protologue. Habitat in Jamaica [*Swartz*].

Pireella panamensis Broth. & Paris *in* Cardot, Rev. Bryol. 40: 18. 1913, invalid name, lacks a description. Based on: Panama. 1900, *F. Hélion* (see Arzeni 1954).

Plants small to medium-sized in dark green or yellow green, thin or dense, frondose masses. Primary stems creeping, with small, erect to imbricate, distantly spaced leaves; rhizoids dark red, smooth to lightly roughened, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions and at base of secondary stems. Secondary stems irregularly spaced, erect, stipitate, densely pinnately or bipinnately branched, to 5 cm long; stems in cross section with sclerodermis of 6–8 rows of small, red, very thick-walled cells, cortical cells enlarged, yellow, thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous. Stipe leaves 1–2 mm long, squarrose-recurved from broadly ovate, clasping bases, narrowed to broad acumina, rounded to the insertions, shortly decurrent; margins serrulate throughout. Secondary stem leaves erect-spreading, not obviously ranked, 2.0–3.0 mm long, broadly ovate-lanceolate, more or less clasping, acuminate, concave, at times lightly rugose when dry, not plicate, rounded to the insertions, shortly decurrent; margins serrulate above, subentire below, plane; costae single, percurrent. Branch leaves erect-spreading to spreading, at times ranked, 1–2 mm long, ovate-lanceolate, gradually acuminate, concave, at times lightly rugose when dry, not plicate, rounded to the insertions, shortly decurrent; margins subentire to lightly serrulate above; costae single, percurrent to subpercurrent; cells smooth or lightly prorate, firm-walled throughout, apical cells fusiform-sigmoid to rounded-rhomboidal, 10–20 × 4–6 μm, median cells fusiform-sigmoid to elongate, 20–34 × 3–5 μm; alar cells not or hardly differentiated, of a few irregularly subquadrate, incrassate, porose cells at the basal angles, cells across the insertions porose, reddish yellow. Asexual gemmae not seen. Dioicous. Perigonia lateral on upper secondary stems and branches. Perichaetial leaves lanceolate-ovate, 5 mm long, abruptly long-acuminate, inner perichaetial leaves abruptly narrowed to long awns; vaginulae hairy. Setae short, smooth, yellowish red, 0.5 mm long. Capsules immersed, erect, symmetric, oval to broadly cylindric, 1.5–2.0 mm long; exothecial cells at mouth red, rounded-quadrate to oblate in 8–10 rows, lower exothecial cells rounded, short-rectangular, firm-walled; stomata absent; opercula conic to rostrate, 0.5–0.8 mm long; annuli rudimentary, of 2–4 rows of firm-walled, quadrate cells; columella pale yellow, thick, 1.5 × 0.75 mm; peristome diplolepideous; exostome teeth 16 or at times united into 8 pairs, deeply inserted within capsule mouth, pale yellow to hyaline, irregularly developed, linear-triangular, to 300 μm long, smooth, weakly trabeculate, prostome well developed; endostome rudimentary. Spores irregularly rounded to ovoid, smooth to lightly roughened, 14–26 μm. Calyptra not seen, "short, mitrate, barely covering the operculum at maturity, scarcely splitting along several lines at base; densely covered by uniseriate hairs, archegonia present" (Newton 1993).

Illustrations. Arzeni (1954, Pl. 19); Duarte Bello (1997, Pl. 190); Buck (1998, Pl. 52 9–15). Figure 72.

Habitat. On tree trunks, branches, and vines; 500–1500 m.

Distribution in Central America. HONDURAS. Atlántida: *Allen 17359* (MO). PANAMA. Chiriquí: *McPherson 8999C* (MO); Darién: *Hammel et al. 16271* (MO, NY); Los Santos: *Croat 34541* (MO); Panamá: *Folsom & Alonzo 5097* (MO).

World range: Central America; Caribbean.

Pireella filicina is a medium-sized species with squarrose-recurved stipe leaves. Its branch leaves are ovate-lanceolate and sometimes ranked. The leaves of *P. filicina* are rounded to the insertion, and the alar cells are weakly to not differentiated. *Pireella filicina* has immersed capsules and short, mitrate calyptrae.

Pireella angustifolia and *P. guatemalensis* are the only other Central American species of *Pireella* with squarrose-recurved stipe leaves. *Pireella guatemalensis* is also similar to *P. filicina* in having ovate-lanceolate branch leaves; it differs, however, in having strongly auriculate stipe and secondary stem leaves. *Pireella angustifolia* is often a larger plant than *P. filicina* and further differs in having narrow, lanceolate branch leaves that are often deciduous. Arzeni (1954), Buck (1998), and Newton

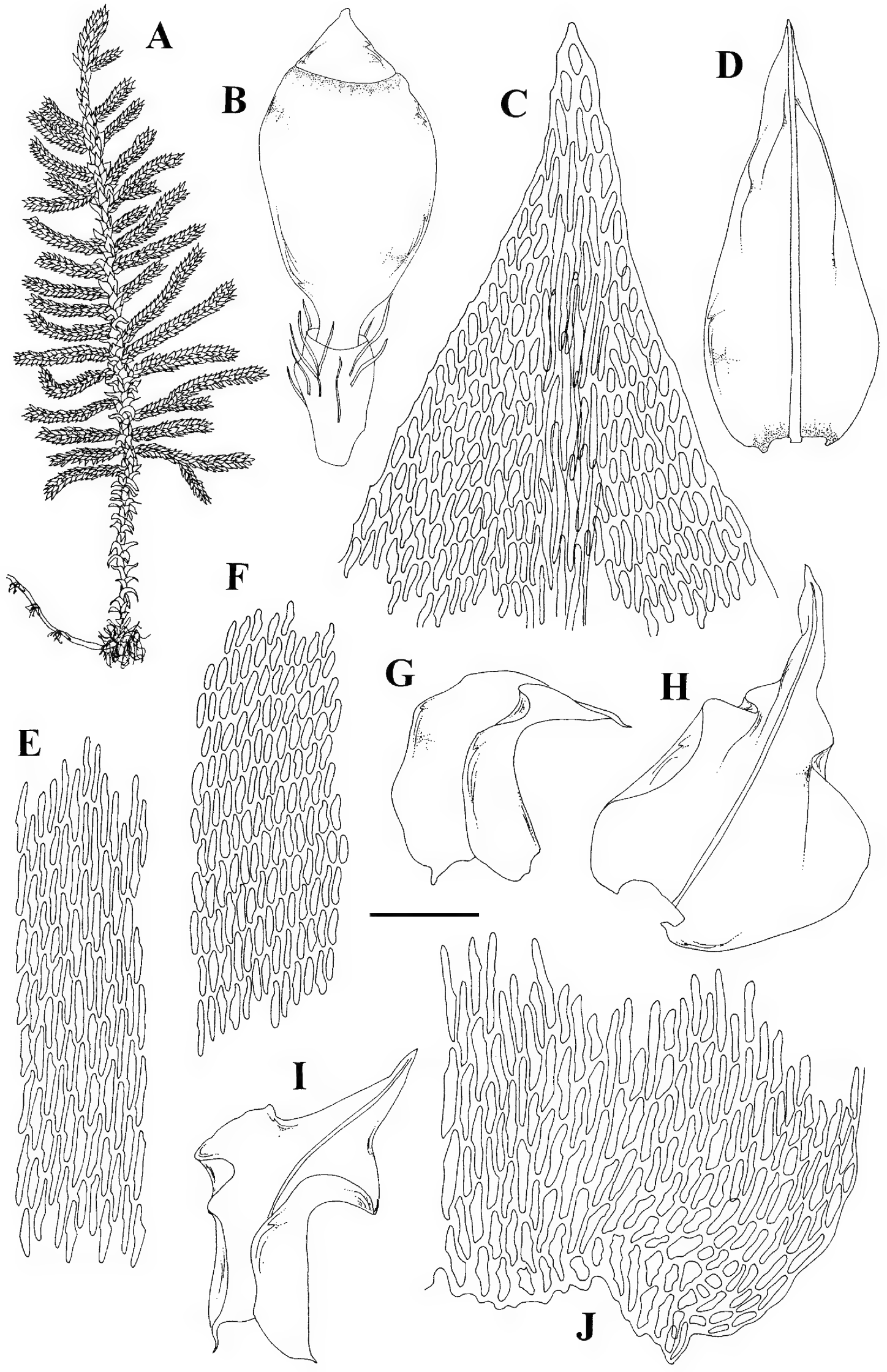
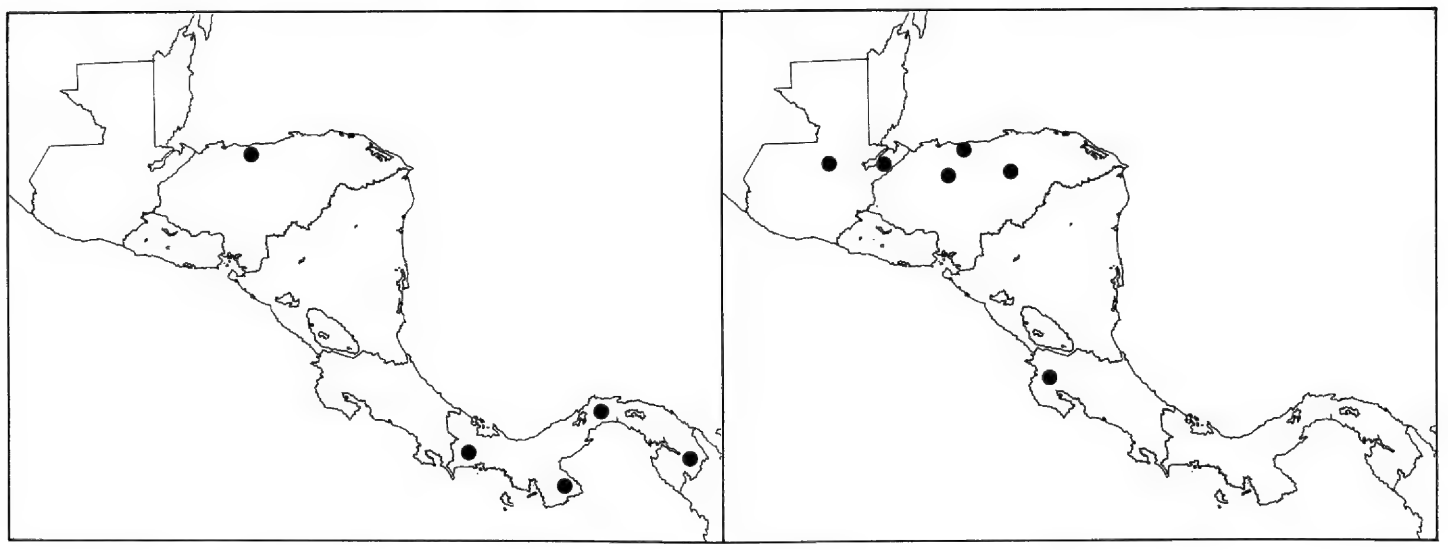


Figure 72. *Pireella filicina*. A. Habit. B. Seta, capsule, and operculum. C. Leaf apex. D. Branch leaf. E. Lower leaf cells. F. Median leaf cells. G & I. Stipe leaves. H. Stem leaf. J. Basal and alar cells. Scale in mm: bar = 0.05 (C, E, F, J); bar = 0.5 (D, G–I); bar = 0.9 (B); bar = 8.0 (A). A from *Croat 34541*; B from *McPherson 8999c*; all other figure parts from *Hammel 16401*.



Pireella filicina *Pireella guatemalensis*

(1993) considered *P. angustifolia* to differ from *P. filicina* in having longer upper leaf cells. As noted by Newton (1993), however, the branch leaf cells of these two species overlap in size, and in Central America the median leaf cells are considerably longer than the mean of 10 μm reported by Newton (1993).

Although it is a dioicous moss, the majority of Central American collections of *P. filicina* are fertile. Their immersed, ovoid to broadly cylindrical capsules with short, mitrate calyptrae are also found in *Pireella angustifolia* and *Pterobryon densum*. Most species of *Pireella* have exserted capsules and large cucullate calyptrae. The presence in these three species of immersed capsules with short mitrate calyptrae may indicate they all belong in *Pterobryon*.

6. *Pireella guatemalensis* R. S. Williams *ex* E. B. Bartram, Bryologist 49: 116. 1946. Protologue. Guatemala. Dept. Alta Verapaz: Finca Mocca, *Harry Johnson 154 in part*. Types. Guatemala. Finca Mocca, Alta Verapaz, *Harry Johnson 154 in part* (F, holotype); Guatemala. Finca Mocca, Alta Verapaz, *Harry Johnson 154*[a] (FH, isotype).

Pireella guatemalensis Broth. *in* Cardot, Rev. Bryol. 40: 18. 1913, invalid name, lacks a description.

Pireella guatemalensis Broth. *in* Arzeni, Amer. Midl. Naturalist 52: 27. 1954, invalid name, listed in synonymy. Based on: Guatemala. Alta Verapaz, Cibilquitz, *Türckheim 6931* (see Newton 1993).

Pireella guatemalensis R. S. Williams *ex* E. B. Bartram var. *mexicana* Arzeni, Amer. Midl. Naturalist 52: 27. 1954. Protologue. Mexico. Oaxaca, Choapam, region of Chinantla, Toabela, San Juan de Petlapa, dense, subtemperate forest on rocky mountain slopes (on rock), Oct. 26, 1944, *J. V. Santos 3431*. Types. Mexico. State of Oaxaca. Dense sub-temperate forest on rocky mountain slopes, Toabela, San Juan de Petlapa. Region of Chinantla, District of Choapam, Collector, *José Vera Santos No. 3431*, 26 October 1944 (FH, holotype; US, isotype).

Plants medium-sized, in dark green or yellow green, thin or dense, frondose masses. Primary stems creeping, with small, erect to imbricate, distantly spaced leaves; rhizoids dark red, smooth to lightly roughened, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions and at base of secondary stems. Secondary stems irregularly spaced, erect, stipitate, densely pinnately or bipinnately branched, 3–6 cm long; stems in cross section with sclerodermis of 6–8 rows of small, red, very thick-walled cells, cortical cells enlarged, yellow, thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous. Stipe leaves squarrose-recurved from broadly ovate, strongly clasping bases, abruptly narrowed to a slender acumina, strongly auriculate, 1–2 mm long. Secondary stem leaves erect-spreading, not obviously ranked, 2.0–2.5 mm long, broadly ovate-lanceolate, clasping, acuminate, concave, at times lightly rugose when dry, not plicate, strongly auriculate; margins denticulate, plane; costae single, subpercurrent; cells smooth, firm- to thick-walled throughout, porose and porose across the insertions, apical cells fusiform-sigmoid to rounded-rhomboidal, 12–24 × 4–5 μm, median cells fusiform-sigmoid, 14–28 × 4–6 μm; alar cells not or hardly differentiated, of a few irregularly subquadrate, incrassate, porose cells at the basal an-

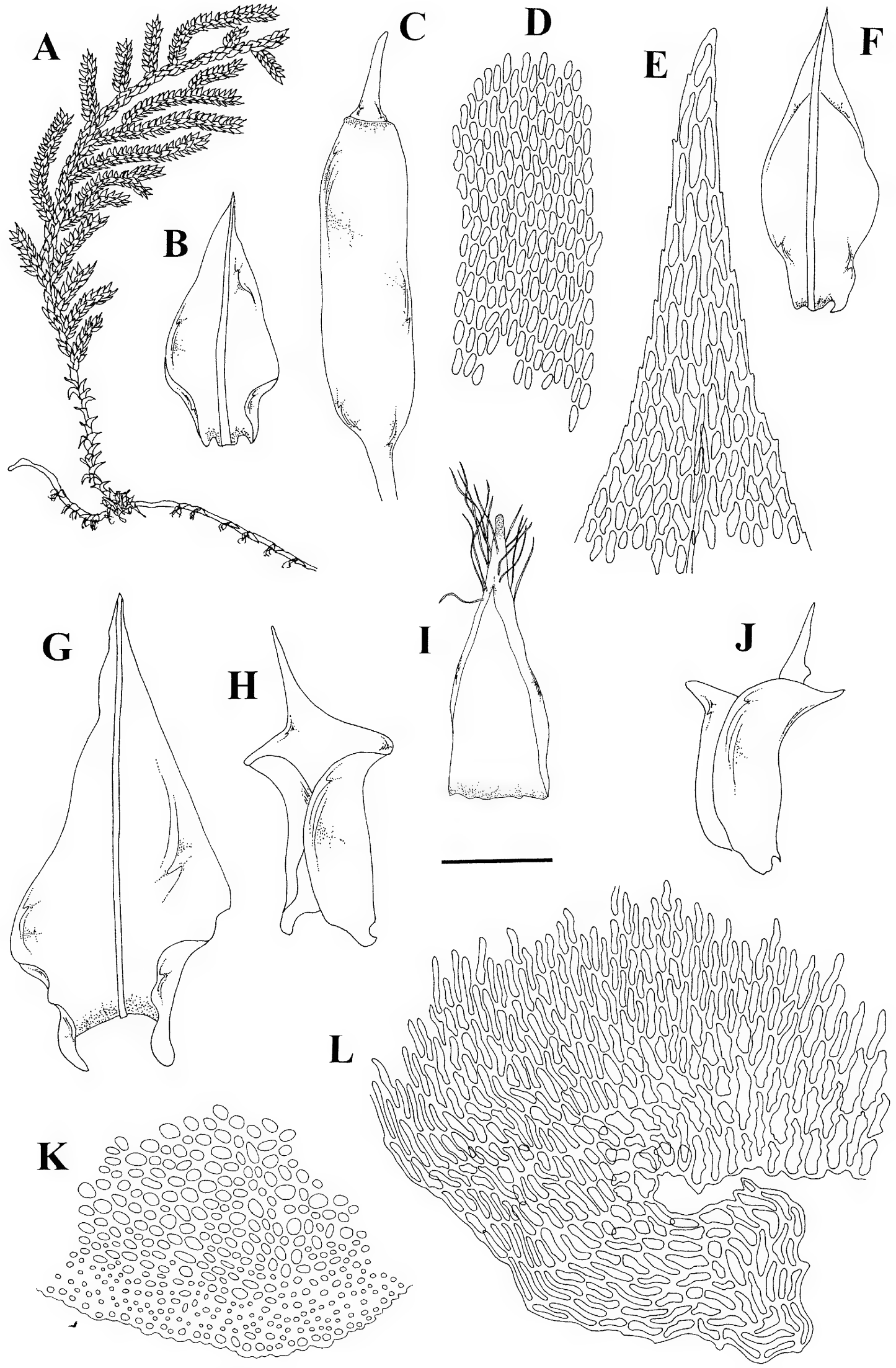


Figure 73. *Pireella guatemalensis*. A. Habit. B & F. Branch leaves. C. Seta, capsule, and operculum. D. Upper leaf cells. E. Leaf apex. G. Stem leaf. H & J. Stipe leaves. I. Calyptra. K. Stem in cross section. L. Basal and alar cells. Scale in mm: bar = 0.06 (D, E, L); bar = 0.08 (K); bar = 0.5 (B, F, G, H, J); bar = 1.25 (C); bar = 1.3 (I); bar = 6.4 (A). All figure parts from *Allen 17466*.

gles, cells in auriculations linear-contorted, cells across the insertions reddish yellow. Branch leaves ovate, 1.0–1.5 mm long, moderately auriculate, otherwise similar to secondary stem leaves. Asexual reproduction by uniseriate, septate gemmae arising from circular clusters of initials in leaf axils. Dioicous. Perigonia lateral on upper secondary stems and branches. Perichaetial leaves lanceolate-ovate, 3 mm long, abruptly long-acuminate; vaginulae densely hairy. Setae elongate, roughened above, red, 5–8 mm long. Capsules exserted, erect, symmetric, cylindric, 1.7–2.5 mm long; exothecial cells at mouth dark red, oblate in 8–10 rows, lower cells short-rectangular or irregularly pentagonal to hexagonal, firm-walled; stomata absent; opercula long-conic to rostrate, 1.0–1.5 mm long; annuli simple, of 2–4 rows of thin-walled, quadrate cells; columella pale yellow, thick, 2.5 mm long; peristome diplolepideous, exostome deeply inserted within capsule mouth, teeth 16 or at times united into 8 pairs, pale yellow to hyaline, irregularly developed, linear-triangular, 120–200 μm long, smooth, weakly trabeculate, prostome well developed; endostome rudimentary. Spores irregularly ovoid to oblong, smooth to lightly roughened, 28–50 μm. Calyptrae cucullate, 2.5–3.0 mm long, hairy.

Illustrations. Bartram (1949, Fig. 115 E–I); Arzeni (1954, Pl. 21); Sharp *et al.* (1994, Fig. 530); Buck (1998, Pl. 53 1–12). Figure 73.

Habitat. On trunks, branches, and twigs of trees, and on vines, occasionally on rocks; 120–1400 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: *Johnson 154a* (F, FH); Izabal: *Steyermark 41890B* (MICH). HONDURAS. Atlántida: *Allen 17466* (MO, TEFH); Olancho: *Allen 12612* (MO); Yoro: *Allen 13633* (MO). COSTA RICA. Guanacaste: *Crosby 3845* (DUKE, MO).

World range: Mexico; Central America; Caribbean.

Pireella guatemalensis is a fairly large species of *Pireella* with squarrose recurved stipe leaves. It has broadly ovate-lanceolate stem leaves and often short, rounded-rhomboidal upper median leaf cells. These leaf cells, however, can also be fusiform-sigmoid, and so leaf cell shape is not a consistently diagnostic feature of the species. The stipe and stem leaves of *P. guatemalensis* are strongly auriculate, and this feature, in combination with its squarrose stipe leaves, is encountered in Central America only in *P. hondurensis*.

Pireella hondurensis differs from *P. guatemalensis* in having distinctly falcate, longer (1.5–2.1 mm vs. 1.0–1.5 mm), often deciduous, lanceolate branch leaves, with strongly prorate, longer (21–30 μm vs. 12–24 μm) upper cells. One of the best features distinguishing the two species is costal length; *P. hondurensis* has costae only two-thirds the leaf length, while those of *P. guatemalensis* are subpercurrent. The two species also have different capsule shapes: orbicular in *P. hondurensis*; cylindrical in *P. guatemalensis*.

Pireella angustifolia and *P. filicina* are the other Central American species of *Pireella* with squarrose stipe leaves. *Pireella angustifolia* differs from *P. guatemalensis* in having lanceolate branch and stem leaves, with consistently elongate, often prorate upper median cells. In addition, most collections of *P. angustifolia* have at least some branches with deciduous leaves, and its capsules are immersed. *Pireella filicina* is similar to *P. guatemalensis* in having ovate-lanceolate stem and branch leaves. Its stem leaves, however, are somewhat decurrent, weakly rounded to the insertions, and with better-developed, subquadrate to rhombic alar cells. Furthermore, the capsules in *P. filicina* are immersed rather than exserted.

7. *Pireella hondurensis* A. E. Newton & B. H. Allen, *sp. nov.* Type. Honduras. Olancho: Sierra de Algalta; La Chorrera, Rio Lara below Montana Bibilonia, 15 km NNW of Catacamas. 14°59′N, 85°56′W, 30 May 1992, *Allen 12614B* (MO, holotype).

Species haec *Pireellae guatemalensi* similis sed foliis ramorum elongatis falcatis lanceolatis, auriculis grandibus, cellulis in partibus foliorum concavis elongatis, costis brevioribus, foliis ramorum caducis setis omnibus scabrosis, capsulisque orbicularis differt.

Plants medium-sized to large, frondose, from creeping stolons, 3.5–8.0 cm high. Stolon leaves short, ovate-acuminate, 0.4 × 0.25 mm, appressed, abruptly narrowed to the acumen; costa absent. Stems stipitate, densely and regularly, bipinnately branched. Stipes 7–18 mm long; lower leaves broadly ovate-acuminate, 1.2–1.6 × 0.65–0.75 mm, abruptly narrowed and recurved to squarrose acumina; base rounded to weakly auriculate; costa absent; upper leaves long ovate-acuminate,

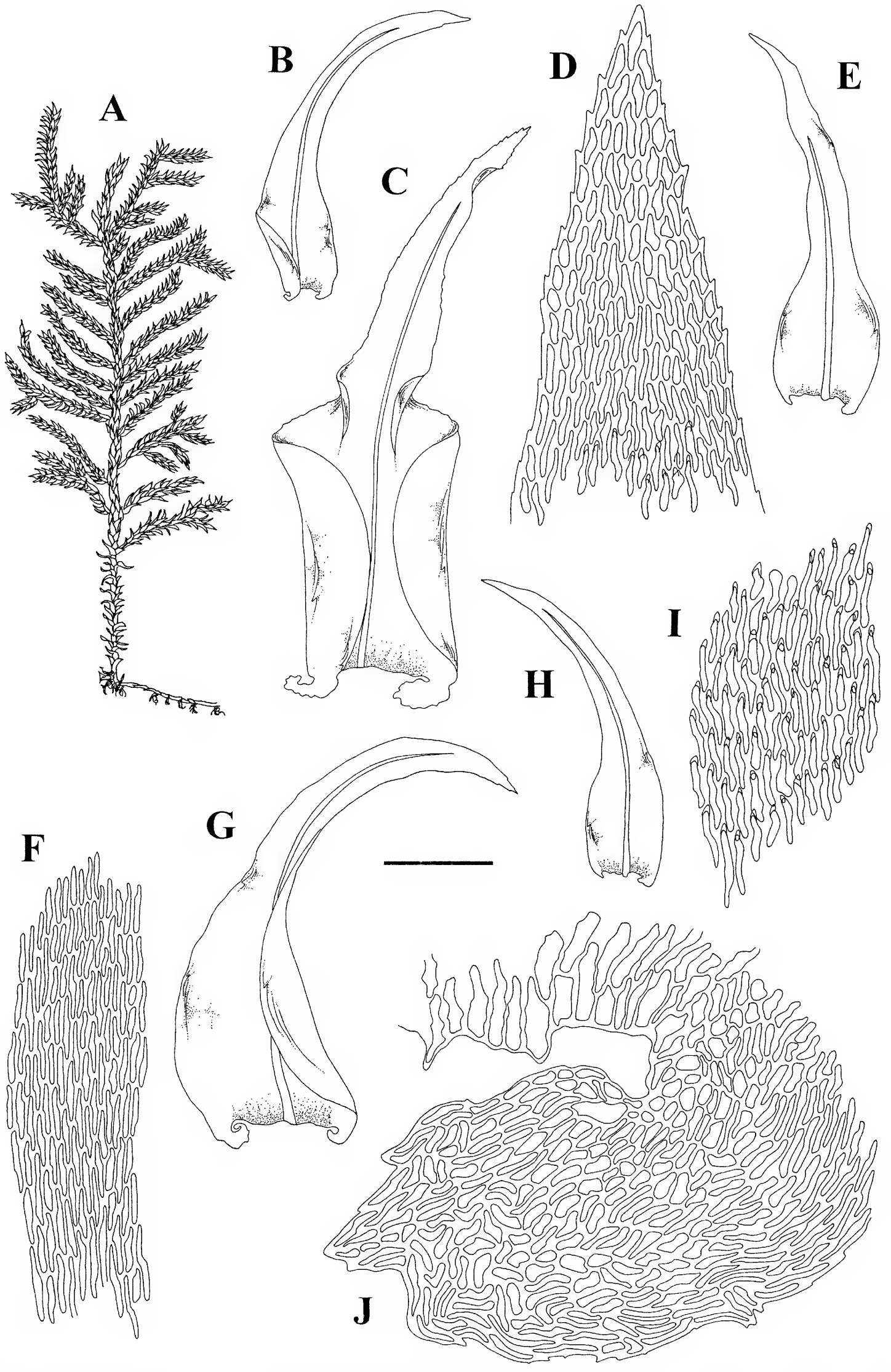
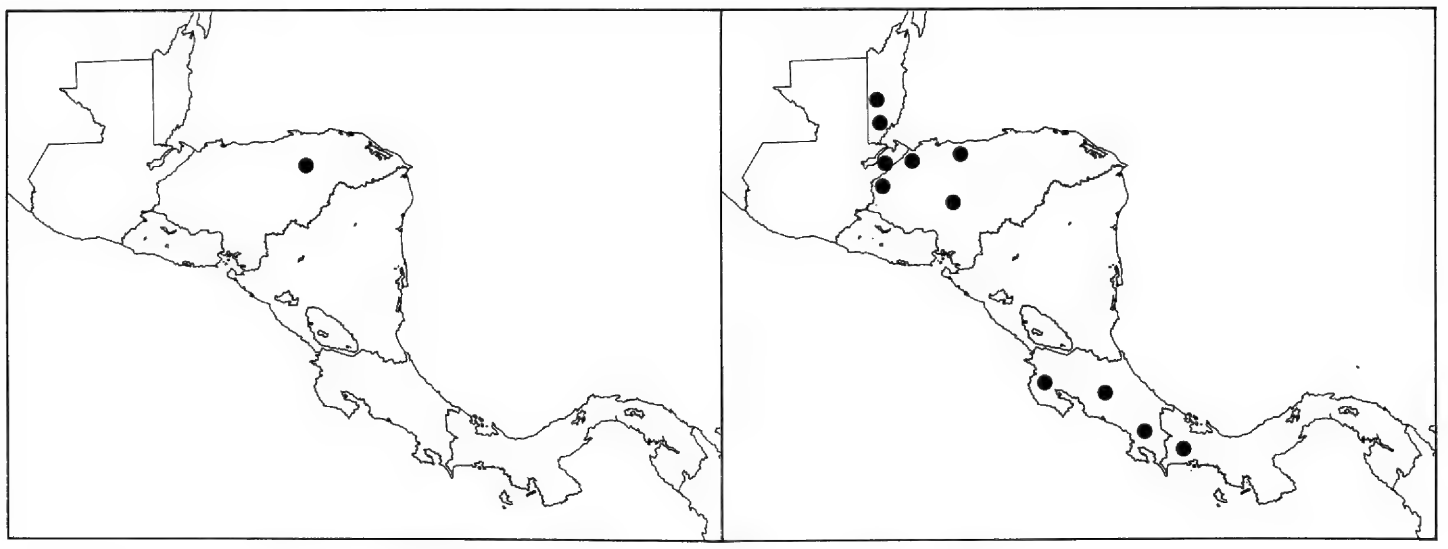


Figure 74. *Pireella hondurensis*. A. Habit. B, E & H. Branch leaves. C. Stipe leaf. D. Leaf apex. F. Median leaf cells. G. Stem leaf. I. Upper leaf cells. J. Basal and alar cells. Scale in mm: bar = 0.06 (D, F, I, J); bar = 0.6 (B, C, E, G, H); bar = 10.0 (A). All figure parts from *Allen 12614B* (type).



Pireella hondurensis *Pireella mariae*

2.9–3.85 × 1.4–1.6 mm, clasping at base, recurved to squarrose, gradually narrowed to long acumina; margins denticulate above; base strongly auriculate; upper cells 16–48 × 3.5 μm, strongly prorate, walls moderately thickened, porose; alar cells numerous, linear and contorted, filling auricles; costae reaching above midleaf. Stem leaves ovate-acuminate, 3.2–4.7 × 1.1–1.4 mm, erect, slightly concave; cells in concave region 18–35 × 5 μm, strongly prorate; upper margins strongly denticulate near apex; costae reaching 2/3 the leaf length. Branch leaves in five weak spiraling rows, lanceolate, falcate, 1.5–2.1 × 0.4–0.5 mm, weakly concave, slightly auriculate; margins erect, flattening out above to form short apical blades, denticulate above; alar cells contorted, filling auricles; cells in concave region 21–30 × 5 μm, strongly prorate, walls thickened, porose below; costa reaching 2/3 the leaf length. Axillary gemmae not seen, asexual reproduction by means of deciduous branch leaves. Dioicous, only female plants known. Perichaetial leaves narrow, ovate-acuminate, 1.2–3.7 × 3–8 mm, abruptly narrowed to acumina, often notched at the shoulders; cells 14–46 × 5 μm, strongly porose, not prorate; costae of inner leaves vanishing in apices; margins of acumina denticulate. Setae elongate, 6.5 mm long, scabrous throughout, with low, warty papillae. Capsules exserted, spheroid, 1.8 × 1.5 mm, mouth small, 0.5 mm; opercula rostrate; peristome obscured, (upper portion missing). Calyptra and spores not seen.

Illustration. Figure 74.
Habitat. On upper trunk of fallen tree; 1100–1800 m.
Distribution in Central America. HONDURAS. Olancho: *Allen 12614B* (MO).
World range: Central America.

Pireella hondurensis is a medium-sized to large species, with stipe leaves that are clasping at base but recurved to squarrose above. The stipe leaves as well as the secondary stem leaves are strongly auriculate at base. The secondary stem and branch leaves are falcate, with strongly prorate upper leaf cells and costae that end in the upper two-thirds of the leaf. Sporophytically, *P. hondurensis* is marked by its elongate, scabrous setae and orbicular capsules.

This species is close to *P. guatemalensis*, sharing with it recurved stipe leaves that have exceptionally large auricles. However, the branch leaves of *P. guatemalensis* are non-deciduous, erect-spreading, ovate, and shorter (1.0–1.5 mm vs. 1.5–2.1 mm) than the often deciduous, falcate, lanceolate leaves of *P. hondurensis*. Furthermore, the upper cells of the branch leaves of *P. guatemalensis* are smooth and shorter (12–24 μm vs. 21–30 μm) than the strongly prorate upper cells of *P. hondurensis*. The best feature that distinguishes the two species is costal length. In *P. guatemalensis* the costae are subpercurrent, while those of *P. hondurensis* reach only two-thirds the leaf length. In addition, the branch leaves of *P. guatemalensis* are not deciduous and their costae end near the apex. The auricles in the stipe and stem leaves of *P. hondurensis* are rather larger than those of *P. guatemalensis* and are also well developed on the branch leaves, where they form small, almost circular lobes at the corner of the leaf. The two species also have different capsule shapes: cylindrical in *P. guatema-*

lensis; orbicular in *P. hondurensis.*

Pireella hondurensis is also close to *P. falcifolia*, which has orbicular capsules on elongate, scabrous setae, long-lanceolate, falcate branch leaves with costae reaching two-thirds the leaf length, and strongly prorate upper leaf cells. *Pireella falcifolia* differs from *P. hondurensis* in having appressed stipe leaves, rounded to weakly auriculate stipe and stem leaves, non-deciduous branch leaves, and relatively short upper cells in the branch leaves (12–30 μm vs. 21–30 μm).

8. *Pireella mariae* (Cardot) Cardot, Rev. Bryol. 40: 18. 1913. *Pirea mariae* Cardot, Bull. Soc. Roy. Bot. Belgique 32(1): 176. 1893. Protologue. [Costa Rica] Forêts de Juan Viñas, versant atlantique, 1135 m, sur les troncs d'arbres (*Pitt*[ier]. *n°* *5653*).

Plants small to medium-sized, in dark green or yellow green, thin or dense, dendroid masses. Primary stems creeping, with small, erect to imbricate, distantly spaced leaves; rhizoids dark red, smooth to lightly roughened, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions and at base of secondary stems. Secondary stems irregularly spaced, erect, stipitate, loosely pinnately or bipinnately branched, to 6 cm long; stems in cross section with sclerodermis of 6–8 rows of small, red, very thick-walled cells, cortical cells enlarged, yellow, thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous. Stipe leaves closely appressed, rounded to auriculate, ovate, somewhat clasping at base, acuminate; margins entire to lightly serrulate; costae absent or reaching midleaf, 1–2 mm long. Secondary stem leaves appressed, not obviously ranked, 2–3 mm long, ovate-lanceolate, more or less clasping, slenderly acuminate, concave, at times lightly rugose when dry, not plicate, rounded to the insertions or auriculate; margins entire to lightly serrulate, plane; costae single, ending below the apex, often wavy above. Branch leaves erect-imbricate, at times weakly ranked, 0.8–1.2 mm long, ovate-lanceolate, short-acuminate, concave, at times lightly rugose when dry, not plicate, rounded to the insertions; margins subentire to lightly serrulate above; costae single, percurrent to subpercurrent; cells smooth, firm-walled throughout, apical cells oval to rounded-rhomboidal, 10–20 × 4–6 μm, median cells oval to rounded-rhomboidal, 10–16 × 4–6 μm; alar cells not or hardly differentiated, of a few irregularly subquadrate, incrassate, porose cells at the basal angles, cells across the insertions porose, reddish yellow. Asexual reproduction by uniseriate, septate gemmae arising from circular clusters of initials in leaf axils. Dioicous. Perigonia lateral on upper secondary stems and branches. Perichaetial leaves oblong-lanceolate, 2–3 mm long, abruptly long-acuminate; vaginulae hairy. Setae elongate, scabrous above, red, 6–9 mm long. Capsules exserted, erect, symmetric, ovoid to subglobose, 2.0–2.5 mm long; exothecial cells at mouth red, rounded-quadrate to oblate in 8–10 rows, lower cells rounded, short-rectangular, firm-walled; stomata absent; opercula conic-rostrate, 1.0–1.5 mm long; annuli simple, of 2–4 rows of firm-walled, quadrate cells; columella pale yellow, thick, 2.2 × 0.75 mm; peristome diplolepideous, exostome deeply inserted within capsule mouth, teeth 16 or at times united into 8 pairs, pale yellow to hyaline, irregularly developed, linear-triangular, to 200 μm long, smooth, weakly trabeculate, prostome well developed; endostome rudimentary. Spores irregularly rounded to oblong, lightly roughened, 20–40 μm. Calyptra cucullate, hairy, 2.0 mm long.

Illustrations. Bartram (1949, Fig. 115 A–D); Arzeni (1954, Pl. 24); Sharp *et al.* (1994, Fig. 531). Figure 75.

Habitat. On tree trunks and old logs; 860–1520 m.

Distribution in Central America. BELIZE. Cayo: *Allen 15040* (MO); Toledo: *Schipp S-867* (NY). GUATEMALA. Izabal: *Steyermark 41890* (FH). HONDURAS. Atlántida: *Allen 17423* (MO, TEFH); Comayagua: *Allen 13745* (MO); Copán: *Allen 17765* (MO, TEFH); Cortés: *Morton 7639* (US). COSTA RICA. Cartago: *Standley 34249* (FH, NY, US); Guanacaste: *Crosby 3857* (MO, NY); Puntarenas: *Crosby 2482* (MO). PANAMA. Chiriquí: *Stevens 18442A* (MO).

World range: Mexico; Central America.

Pireella mariae is a medium-sized species with erect-appressed stipe leaves. The secondary stem leaves are considerably larger and morphologically different than the branch leaves, and the costae in both are often wavy above. The branch leaves have short, mostly oval median cells and nearly undif-

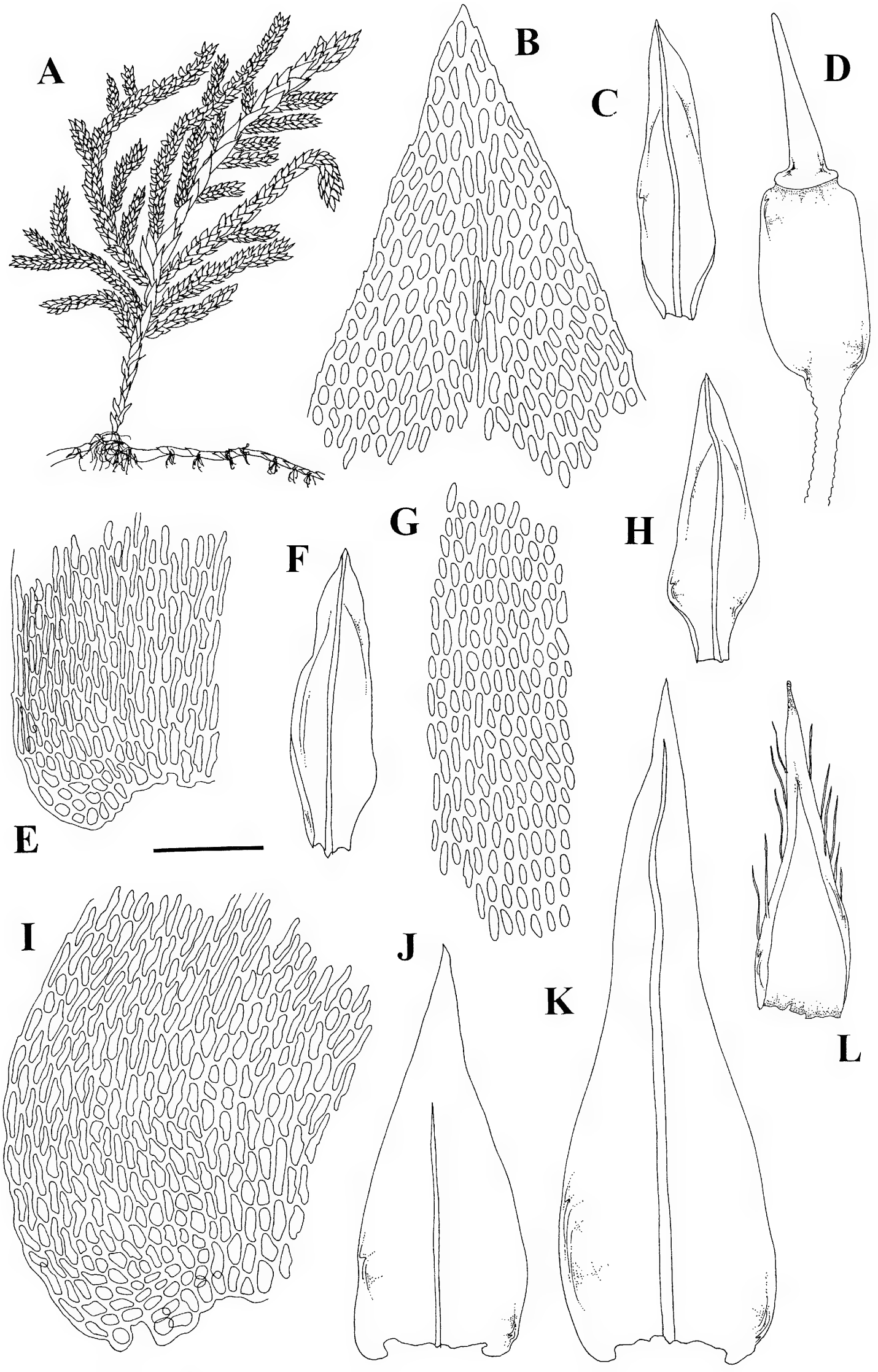


Figure 75. *Pireella mariae*. A. Habit. B. Leaf apex. C, F & H. Branch leaves. D. Seta, capsule, and operculum. E. Branch leaf basal and alar cells. G. Median leaf cells. I. Stem leaf basal and alar cells. J. Stipe leaf. K. Stem leaf. L. Calyptra. Scale in mm: bar = 0.06 (B, E, G, I); bar = 0.5 (C, F, H, J, K); bar = 0.9 (D, L); bar = 5.1 (A). D, L from *Allen 17769*; all other figure parts from *Allen 15040*.

ferentiated alar cells. The capsules of *P. mariae* are ovoid to subglobose and long-exserted. The setae are scabrous in the upper half, and the calyptrae are large, cucullate, and sparsely hairy.

Pireella pycnothallodes is the only Central American species of *Pireella* that can be confused with *P. mariae*, because both have erect-appressed stipe leaves, branch leaves with short median leaf cells, and often wavy costae. In *P. pycnothallodes*, however, the leaves have numerous rows of the small, quadrate alar cells that give them an aspect more similar to *Cryphaea* than *Pireella*. Furthermore, the secondary stem and branch leaves in *P. pycnothallodes* are more or less similar in size, and the lower leaf margins are at times tightly recurved. Sporophytically, *P. pycnothallodes* differs from *P. mariae* in having long-cylindric capsules and smooth setae.

9. *Pireella papillosula* (Renauld & Cardot) Renauld & Cardot, Rev. Bryol. 40: 18. 1913. *Pirea papillosula* Renauld & Cardot, Rev. Bryol. 37: 7. 1910. Protologue. Mexique, sans indication de localité (*Maury*; herb. F. Renauld).

Pilotrichella nana Hampe *ex* Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32(1): 177. 1894, invalid name, lacks a description. Based on *Hampe 1881* (BM) (see Newton 1993).

Plants small, in light green or yellow green, thin or dense, frondose masses. Primary stems creeping, with small, erect to imbricate, distantly spaced leaves; rhizoids dark red, smooth to lightly roughened, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions and at base of secondary stems. Secondary stems 1.5–3.0 cm long, irregularly spaced, erect, stipitate, bipinnately branched; stems in cross section with sclerodermis of 3–6 rows of small, red to orange brown, very thick-walled cells, cortical cells enlarged, hyaline to yellowish, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous. Stipe leaves erect to erect-appressed, ovate-triangular to oblong-ovate, 0.7–1.2 mm long, rounded to insertion, shortly decurrent, abruptly acuminate; margins serrulate above, narrowly recurved above, or at times throughout; costae percurrent; upper cells linear, prorate; alar cells weakly developed, of a few subquadrate to short-rectangular cells on the inner margin of the auricle. Secondary stem leaves erect, 1.0–1.5 mm long, ovate-acuminate, clasping at base, gradually acuminate, concave, not plicate, rounded to the insertions, shortly decurrent; margins denticulate to serrulate; costae single, percurrent; alar cells weakly developed, of a few subquadrate to short-rectangular cells on the inner margin of the auricle. Branch leaves erect to erect-spreading, spirally ranked, ovate-lanceolate to lanceolate, 0.8–1.3 mm long, concave, not plicate, rounded to the insertions, decurrent; margins serrulate, erect to plane; costae single, percurrent to subpercurrent; cells distinctly prorate, firm-walled throughout, occasionally porose, apical cells elongate-sigmoid, 16–26 × 3–5 μm, median cells in concave part of leaf elongate-sigmoid, 16–25 × 3–5 μm; alar cells hardly developed, of a few subquadrate cells at the basal angles, cells across the insertions often porose, reddish yellow. Asexual gemmae not seen. Dioicous. Sporophytes not seen, description from Newton (1993). Perichaetial leaves ovate-acuminate, 2–3 mm long, abruptly long-acuminate, often notched at the shoulders; vaginulae hairy. Setae elongate, yellow brown to orange brown, 6–8 mm long. Capsules exserted, erect, symmetric, cylindrical, 1.9–2.3 mm long; opercula short-rostrate, 1.0 mm long; peristome diplolepideous, irregularly developed, to 170 μm long, inserted within the mouth; exostome teeth 16, thin and delicate, prostome well developed; endostome rudimentary. Spores round, 23 μm. Calyptra cucullate, sparsely hairy.

Illustrations. Buck (1998, Pl. 54 8–15). Figure 76.

Habitat. On tree trunks; 50–900 m.

Distribution in Central America. BELIZE. Cayo: *Allen 18472A* (MO). GUATEMALA. Petén: *Lundell 2867* (FH, US). HONDURAS. Cortés: *Morton 7639b* (US).

World range: Mexico; Central America; Caribbean.

Pireella papillosula is a small species with regularly pinnately branched secondary stems. It has erect stipe leaves with margins that are narrowly recurved in the upper half or sometimes throughout. The branch leaves of *P. papillosula* are ovate-lanceolate to lanceolate with weakly developed alar cells and elongate-sigmoid upper cells that are typically distinctly prorate.

Pireella angustifolia has sometimes been confused with *P. papillosula*, because both species have regularly branched secondary stems, narrow branch leaves, and elongate, often prorate upper leaf

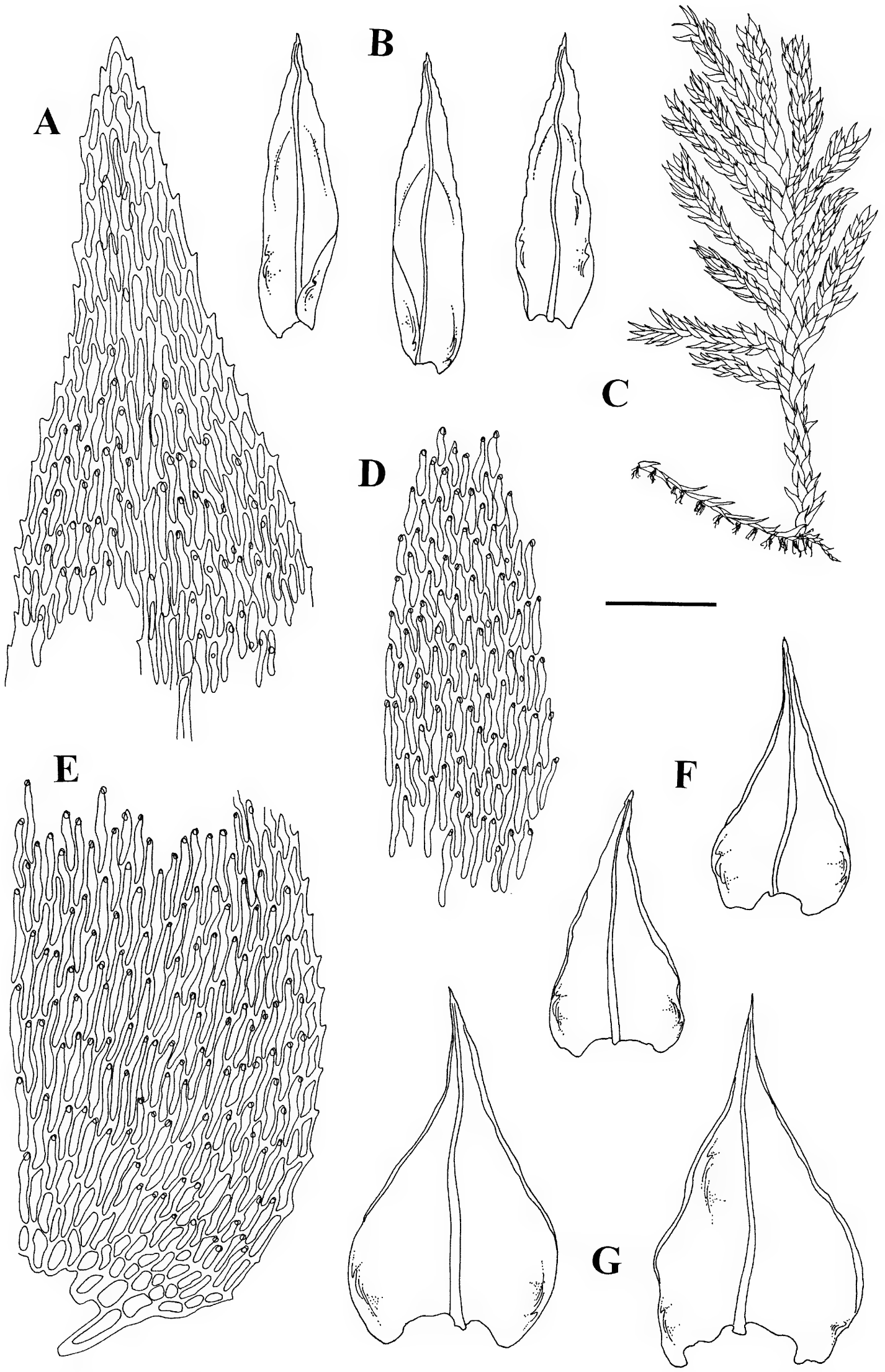
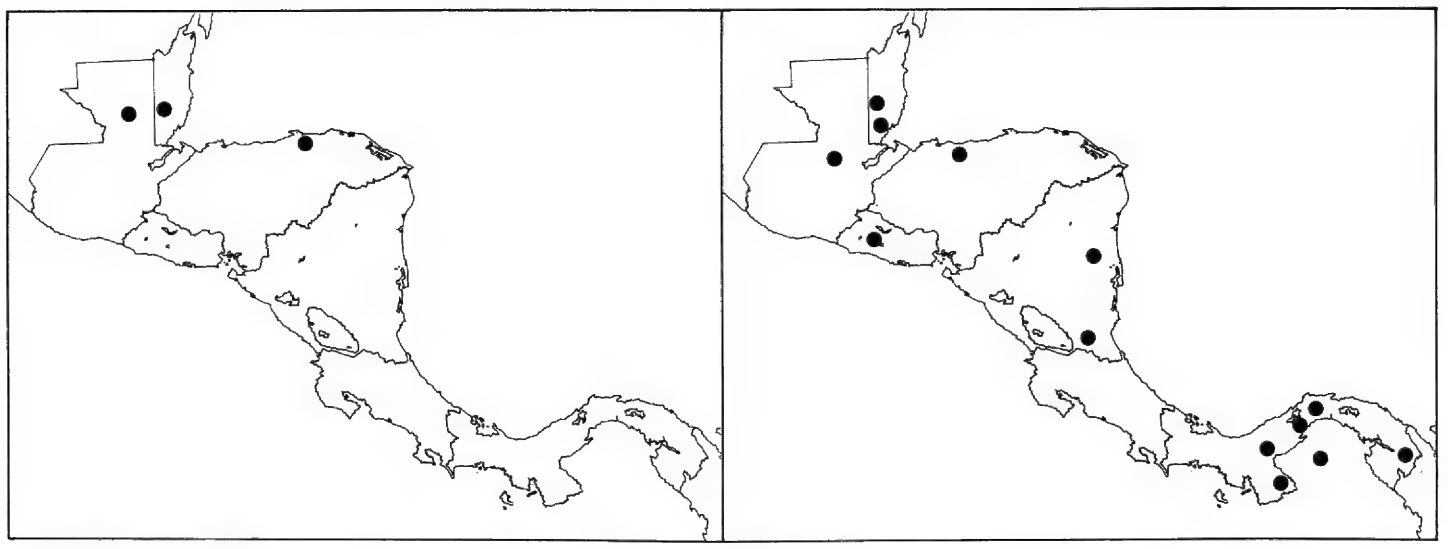


Figure 76. *Pireella papillosula*. A. Leaf apex. B. Branch leaves. C. Habit. D. Upper leaf cells. E. Basal and alar cells. F. Stipe leaves. G. Stem leaves. Scale in mm: bar = 0.05 (A, D, E); bar = 0.4 (B, F, G); bar = 2.6 (C). All figure parts from *Allen 18472A*.



Pireella papillosula *Pireella pohlii*

cells. That species, however, is usually much larger than *P. papillosula* (3–10 cm vs. 1.5–3 cm long), and further differs in having plane-margined, squarrose stipe leaves.

Pireella cymbifolia and *P. pohlii* are similar to *P. papillosula* in size. All three species also have erect or appressed stipe leaves and elongate-sigmoid, usually strongly prorate, upper branch leaf cells. *Pireella cymbifolia* differs from *P. papillosula* in having unbranched or weakly branched secondary stems and numerous quadrate alar cells that extend 6–10 cells up the basal margins. *Pireella pohlii* is sometimes considered synonymous with *P. papillosula* (Arzeni 1954; Magill 1994). The species are very similar, but *P. pohlii* is usually a larger plant (2–10 cm vs. 1.5–3.0 cm long) than *P. papillosula*, it has less regularly branched secondary stems, and the stipe leaves are plane-margined.

10. *Pireella pohlii* (Schwägr.) Cardot, Rev. Bryol. 40: 18. 1913. *Leucodon pohlii* Schwägr., Sp. Musc. Frond. Suppl. 3(1): 232. 1828. *Neckera pohlii* (Schwägr.) Müll. Hal., Syn. Musc. Frond. 2: 114. 1850. *Pterobryon pohlii* (Schwägr.) Mitt., J. Linn. Soc., Bot. 12: 426. 1869. *Pilotrichella pohlii* (Schwägr.) Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32(1): 177. 1894. *Pirea pohlii* (Schwägr.) Broth. *ex* Paris, Index Bryol., ed. 2, 4: 18. 1905. Protologue. In Brasilia legit et dedit *D. Pohl.*

Pilotrichum filicinum (Hedw.) P. Beauv. var. *longipes* Mont., Ann. Sci. Nat., Bot., sér. 2, 14: 339. 1840. Protologue. [French Guiana] Hab. ad ramulos dumetorum in sylvis humidis Guianae, Septembri 1837, lecta.–*Lepr.*[*ieur*] Coll. *n. 323.*

Neckera longipes Müll. Hal., Syn. Musc. Frond. 2: 123. 1850. *Pilotrichella longipes* (Müll. Hal.), A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 254. 1877. Protologue. [French Guiana and Trinidad] Guiana: Hb. Mont. Insula Trinidad Antillarum, Uraruga et Carani Woods, 20 Oct. 1847. Types. Trinidad, Uraruga et Carani Woods, *Crüger* (BM, lectotype, designated here); Guiana: Hb. Mont (syntype, not seen).

Pilotrichum longipes Mont. *ex* Müll. Hal., Syn. Musc. Frond. 2: 123. 1850, invalid name, listed in synonymy.

Neckera ludoviciana Müll. Hal. *in* Mohr, Bull. Torrey Bot. Club 5: 50. 1874. *Pilotrichella ludoviciana* ["*ludowiciana*"] (Müll. Hal.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 254. 1877. Protologue. [United States] S.A. Patria Ludovicia. In sylvis umbrosis prope Baton Rouge, *Dr. Joor* legit. Vere, 1873. Ex herb. C. Mohr.

Neckera ludoviciae Müll. Hal., Flora 58: 92. 1875. *Pterobryon ludoviciae* (Müll. Hal.) Kindb., Canad. Rec. Sci. 6: 19. 1894. *Pirea ludoviciae* (Müll. Hal.) Broth., Nat. Pflanzenfam. I(3): 796. 1906. *Pireella ludoviciae* (Müll. Hal.) Grout, Moss Fl. N. Amer. 3: 216. 1934, not *Pireella ludoviciae* (Müll. Hal.) Cardot, Rev. Bryol. 40: 17. 1913, invalid name, listed in synonymy. Protologue. [United States] S.A. Patria. Louisiana, ad truncos putridos sylvestres prope Batonrouge cum *Hypno biventroso*: *Dr. Joor* Febr. 1874 sterile legit Hb. C. Mohr.

Pilotrichella tonduzii Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32(1): 182. 1894. *Pirea tonduzii* (Renauld & Cardot) Broth., Nat. Pflanzenfam. I(3): 796. 1906. *Pireella tonduzii* (Renauld & Cardot) Cardot, Rev. Bryol. 40: 18. 1913. Protologue. [Costa Rica] Boruca (*Pitt.*[*ier*] *n° 5622*).

Pilotrichum ludoviciae A. Jaeger *ex* Arzeni, Amer. Midl. Naturalist 52: 34. 1954, invalid name, lacks a description.

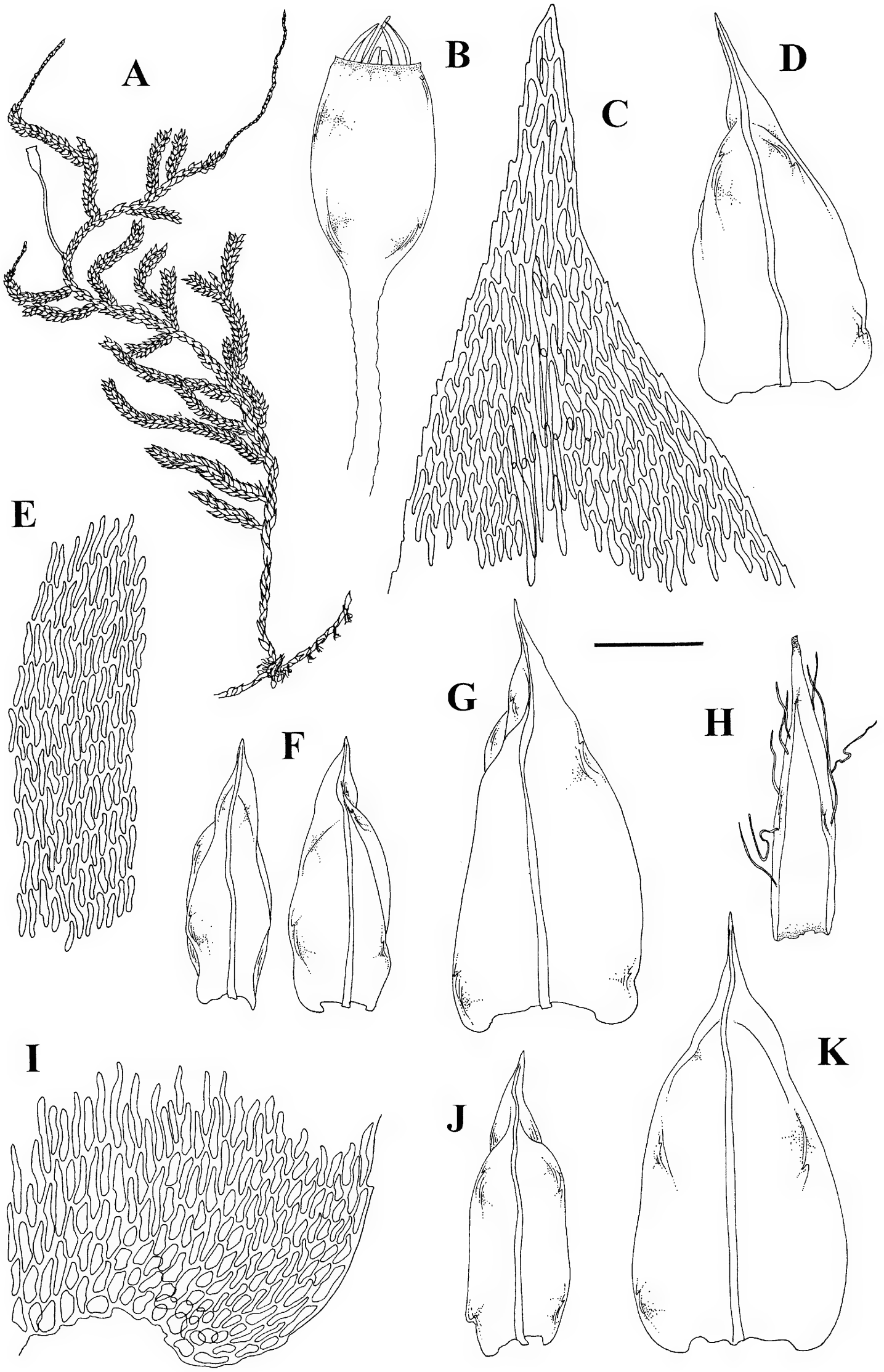


Figure 77. *Pireella pohlii*. A. Habit. B. Seta and capsule. C. Leaf apex. D. Stipe leaf. E. Median leaf cells. F & J. Branch leaves. G & K. Stem leaves. H. Calyptra. I. Branch leaf basal and alar cells. Scale in mm: bar = 0.05 (C, E, I); bar = 0.5 (D, F, G, J, K); bar = 0.9 (B, H); bar = 6.4 (A). All figure parts from *Allen 8754*.

Plants medium-sized to large, in light green or yellow green, thin or dense, frondose masses. Primary stems creeping, with small, erect to imbricate, distantly spaced leaves; rhizoids dark red, smooth to lightly roughened, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions and at base of secondary stems. Secondary stems 2–10 cm long, irregularly spaced, erect, stipitate, irregularly pinnately branched, at times with flagellate branches; stems in cross section with sclerodermis of 3–7 rows of small, red to orange brown, very thick-walled cells, cortical cells enlarged, hyaline to yellowish, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous. Stipe leaves erect to erect-appressed, ovate-triangular to oblong-ovate, 1.5–2.5 mm long, rounded to auriculate at base, decurrent, abruptly acuminate; margins serrulate; costae percurrent to subpercurrent; alar cells weakly developed, of a few subquadrate to short-rectangular cells on the inner margin of the auricle. Secondary stem leaves erect, 2.0–2.5 mm long, ovate, clasping at base, narrowly acuminate, concave, not plicate, rounded to auriculate at the insertions, decurrent; margins subserrulate to serrulate, plane; costae single, subpercurrent to percurrent, often wavy above; alar cells weakly developed, of a few subquadrate to short-rectangular cells on the inner margin of the auricle. Branch leaves erect to erect-spreading, distinctly ranked, ovate-lanceolate, 1.0–1.5 mm long, broadly acuminate, strongly concave, not plicate, rounded to the insertions, decurrent; margins serrulate, erect to plane; costae single, percurrent to subpercurrent; cells prorate, thin- or firm-walled throughout, occasionally porose, apical cells elongate-sigmoid, 16–26 × 3–5 μm, median cells in concave part of leaf elongate-sigmoid, 16–25 × 3–5 μm; alar cells hardly developed, of a few subquadrate cells at the basal angles, cells across the insertions often porose, reddish yellow. Asexual reproduction by uniseriate, septate gemmae arising from circular clusters of initials in leaf axils. Dioicous. Perigonia lateral on upper secondary stems and branches, 1 mm long. Perichaetial leaves ovate-lanceolate, 2–3 mm long, abruptly long-acuminate, inner leaves setaceous; vaginulae hairy. Setae elongate, roughened-papillose, orange brown to red, 6–10 mm long. Capsules exserted, erect, symmetric, cylindrical, 2.0–2.5 mm long; exothecial cells at mouth red, rounded-quadrate to oblate in 8–10 rows, lower cells rounded, subquadrate to short-rectangular, firm- to thick-walled; stomata absent; opercula conic-rostrate, 1.0 mm long; annuli simple, of 2–4 rows of firm-walled, quadrate cells; peristome diplolepideous, exostome inserted within capsule mouth, teeth 16 or at times united into 8 pairs, pale yellow to hyaline, irregularly developed, linear, to 400 μm long, smooth, weakly trabeculate, prostome well developed; endostome rudimentary. Spores irregularly rounded to oblong, roughened-papillose, 22–34 μm. Calyptrae cucullate, hairy, 2.5 mm long.

Illustrations. Schwägrichen (1828, Pl. 232); Grout (1934, Pl. 57 A, as *Pireella ludoviciae*); Bartram (1949, Fig. 114 D–F, as *Pireella cymbifolia*); Arzeni (1954, Pls. 28–29); Breen (1963, Pl. 109 1–4); Florschütz (1964, Fig. 99); Crum and Anderson (1981, Fig. 382); Reese (1984, Fig. 43 O–R); Sharp *et al.* (1994, Fig. 534); Churchill and Linares (1995, Fig. 167 h–k); Duarte Bello (1997, Pl. 192); Buck (1998, Pl. 55 1–7); Gradstein *et al.* (2001, Fig. 195 K–O); Buck (2003, Fig. 115 A–G). Figure 77.

Habitat. On tree trunks and vines; 100–1440 m.

Distribution in Central America. BELIZE. Cayo: *Allen 18384* (BRH, MO); Toledo: *Whittemore 5656* (MO). GUATEMALA. Alta Verapaz: *Steyermark 44995b* (F, FH). EL SALVADOR. Cuscatlán: *Calderón 1996* (NY, US). HONDURAS. Atlántida: *Allen 17316* (MO, TEFH). NICARAGUA. Río San Juan: *Seymour 6201* (MO); Zelaya: *Stevens 12248* (MO). PANAMA. Canal Zone: *Dodge 16617* (FH, MO); Coclé: *Hunter & Allen* (US); Darién: *Allen 8754* (MO); Los Santos: *McPherson 13508* (MO, PMA); Panamá: *Crosby 4550A* (MO), San José Island: *Johnson* (F, FH, NY).

World range: Southeastern U.S.A.; Mexico; Central America; Caribbean; Western, Northern, and Southern South America, Brazil.

Pireella pohlii, the most widely distributed species in the genus, occurs from southern United States to Paraguay. It is a medium-sized species, with erect to erect-appressed stipe leaves and irregularly pinnately branched stems. The branch leaves of *P. pohlii* are ovate-lanceolate and strongly rounded to the insertions, while the stem and stolon leaves are often auriculate. The leaf cells in the upper median region of the leaf concavity are elongate-sigmoid and distinctly prorate, while the alar cells are weakly differentiated, of only a few subquadrate cells in the basal angles of the leaves. *Pireella pohlii* has elongate setae, cylindrical capsules, and large, hairy, cucullate calyptrae.

Pireella cymbifolia has often been confused with *P. pohlii*, because both species have erect stipe leaves, elongate-sigmoid, strongly prorate cells in the upper, median region of the leaf concavity, elongate setae, cylindrical capsules, and large, cucullate calyptrae. *Pireella cymbifolia* differs from *P. pohlii* in having mostly unbranched stems, stem and stipe leaves that are straight at the insertions, and exceptionally well-developed alar cells that consist of numerous rows of quadrate to subrectangular cells.

Pireella papillosula has been treated as a synonym of *P. pohlii* (Arzeni 1954). The two species are similar in having erect stipe leaves as well as branch leaves that are rounded to the insertions, with weakly differentiated alar cells and elongate-sigmoid, prorate cells in the upper, median region of the leaf concavity. *Pireella papillosula*, however, is generally a smaller plant than *P. pohlii*, with regularly bipinnately branched secondary stems and stipe leaves with recurved margins.

11. *Pireella pycnothallodes* (Müll. Hal.) M. Fleisch., Hedwigia 59: 213. 1917. *Dusenia pycnothallodes* Müll. Hal., Hedwigia 36: 107. 1897. Protologue. [Guatemala] Tikál, ad arbores: *Bernoulli et Cario* 1878. Type. Ruina de Tikál. Dep. Petén, ad arbores, Sept. 77, Herbarium Guatemalense N° 54, coll. *Bernoulli & Cario* (S, isotype).

Pirea pachyclada Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 41(1): 67. 1905. *Pireella pachyclada* (Renauld & Cardot) Cardot, Rev. Bryol. 40: 18. 1913. Protologue. Mexique: Yucatan, San-Geronimo (*Morelet*, 1847; sine nomine comm. Bescherelle).

Pireella cubensis Cardot & Thér. *ex* Thér., Mem. Soc. Cub. Hist. Nat. "Felipe Poey" 14: 356. 1940. Protologue. [Cuba] San Diego de los Baños (*Van Hermann 3182*), typus.

Neolindbergia flagellifera Thér., Mem. Soc. Cub. Hist. Nat. "Felipe Poey" 14: 359. 1940. Protologue. [Cuba] Sumidero, in Sierra Caliente, Pinar del Río, sur rochers ombragés (et problablement mouillés ?), leg. *E. L. Ekman 18,197*.

Plants small to medium-sized, in dark green or yellow green, thin or dense, frondose masses. Primary stems creeping, with small, erect to imbricate, distantly spaced leaves; rhizoids dark red, smooth to lightly roughened, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions and at base of secondary stems. Secondary stems irregularly spaced, erect, stipitate, pinnately or bipinnately branched, to 6 cm long; stems in cross section with sclerodermis of 6–8 rows of small, red to orange brown, very thick-walled cells, cortical cells enlarged, hyaline to yellowish, firm- to thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous. Stipe leaves appressed, broadly triangular-ovate, 1–2 mm long, rounded at base, decurrent, acuminate; margins subentire to lightly serrulate, often tightly recurved; costae percurrent to subpercurrent; alar cells quadrate, in numerous rows. Secondary stem leaves erect, not obviously ranked, 1–2 mm long, broadly ovate-lanceolate, more or less clasping, gradually acuminate, concave, not plicate, rounded to the insertions, decurrent; margins entire to lightly serrulate, plane; costae single, percurrent to shortly excurrent, often wavy above; alar cells quadrate, in numerous rows. Branch leaves erect to erect-spreading, at times weakly ranked, ovate to ovate-lanceolate, 1.0–1.5 mm long, broadly or narrowly acuminate, concave, not plicate, somewhat rounded to the insertions, decurrent; margins subentire to lightly serrulate above, erect to plane; costae single, percurrent to subpercurrent; cells smooth, firm-walled throughout, occasionally porose, apical cells oval to rounded-rhomboidal, occasionally elongate, 7–15(–24) × 4–6 μm, median cells in concave part of leaf oval to rounded-rhomboidal, 5–15 × 4–6 μm; alar cells quadrate, in numerous rows, cells across the insertions porose, reddish yellow. Asexual reproduction by uniseriate, smooth, septate gemmae arising from circular clusters of initials in leaf axils, on germination cells smaller and densely papillose. Dioicous. Perigonia lateral on upper secondary stems and branches, 1 mm long. Perichaetial leaves ovate-lanceolate, 2–3 mm long, abruptly long-acuminate, inner leaves setaceous; vaginulae hairy. Setae elongate, scabrous above, yellow, becoming red with age, 2–4 mm long. Capsules exserted, erect, symmetric, cylindrical, 2.0–2.5 mm long; exothecial cells at mouth red, rounded-quadrate to oblate in 8–10 rows, lower cells rounded, short-rectangular, firm- to thick-walled; stomata absent; opercula conic-rostrate, 1.0 mm long; annuli simple, of 2–4 rows of firm-walled, quadrate cells; columella hyaline, slender, 2.0 × 0.2 mm; peristome diplolepideous, exostome deeply inserted within capsule mouth, teeth 16, pale yellow to hyaline, irregularly developed, linear-triangular, to 180 μm long, smooth, weakly trabeculate, pro-

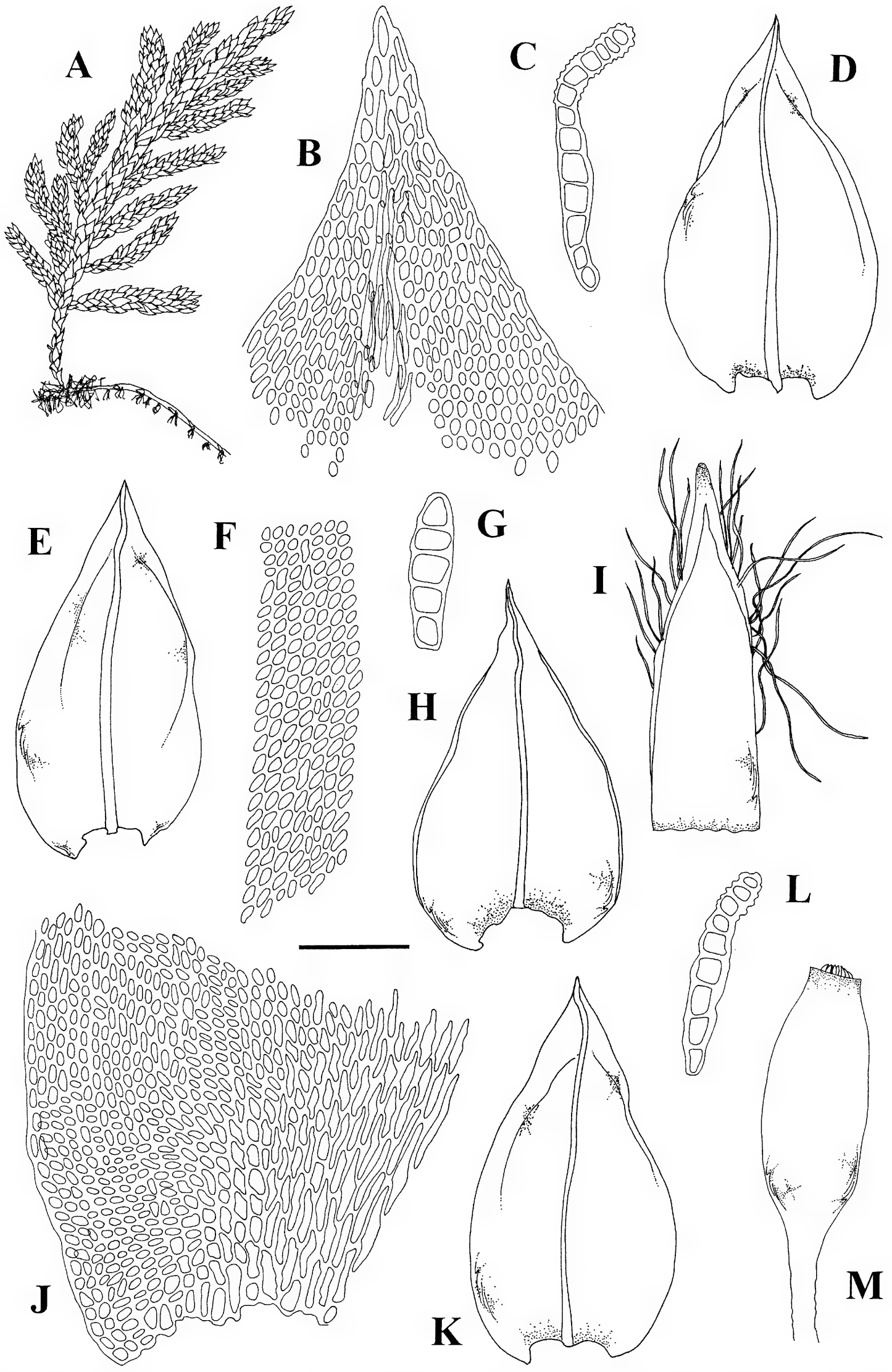
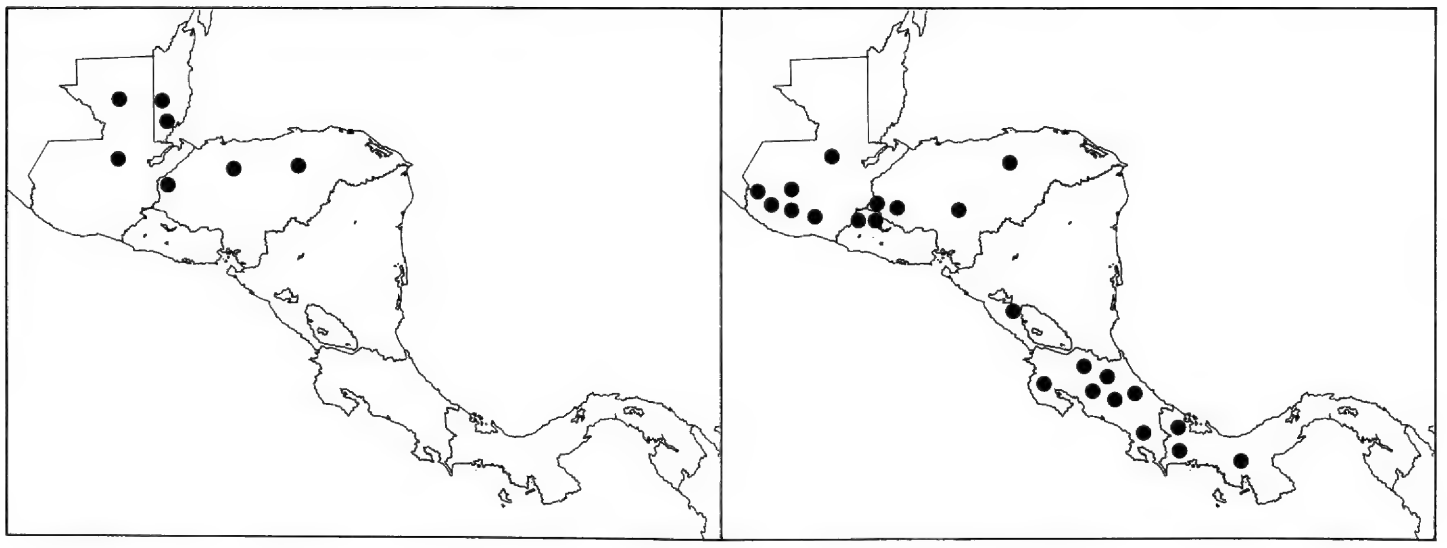


Figure 78. *Pireella pycnothallodes*. A. Habit. B. Leaf apex. C, G & L. Gemmae. D & K. Stem leaves. E. Branch leaf. F. Median leaf cells. H. Stipe leaf. I. Calyptra. J. Basal and alar cells. M. Seta and capsule. Scale in mm: bar = 0.06 (B, C, F, G, J, L); bar = 0.4 (D, E, H, K); bar = 1.0 (I, M); bar = 4.0 (A). A, M from *Allen 18126*; C, G, L from *Allen 18039*; all other figure parts from *Bernoulli & Cario* (type).



Pireella pycnothallodes *Pterobryon densum*

stome well developed; endostome rudimentary. Spores irregularly rounded to oblong, lightly roughened, 30–36 μm. Calyptra cucullate, hairy, 3.0 mm long.

Illustrations. Bartram (1949, Fig. 114 G–J); Arzeni (1954, Pls. 16 & 17); Sharp *et al.* (1994, Fig. 532); Duarte Bello (1997, Pl. 191); Buck (1998, Pl. 54 1–7). Figure 78.

Habitat. On tree trunks and roots, rotting logs, occasionally on limestone; 300–800 m.

Distribution in Central America. BELIZE. Cayo: *Allen 18039* (BRH, MO); Toledo: *Davidse & Brant 32119* (MO). GUATEMALA. Alta Verapaz: *Croat 41549* (MO); Petén: *Lundell 2942* (F, FH, MO, US). HONDURAS. Copán: *Allen 17685* (MO, TEFH); Olancho: *Allen 12904* (MO); Yoro: *Allen 13622* (MO).

World range: Mexico, Central America; Caribbean.

Pireella pycnothallodes is a medium-sized species with usually regularly branched stems and erect to appressed stipe leaves. The secondary stem and branch leaves are more or less similar in size, and typically both are ovate. The upper median leaf cells in the region of the leaf concavity in the branch leaves of *P. pycnothallodes* are consistently oval and firm- to thick-walled. There are, however, some collections of *P. pycnothallodes* that have narrowly ovate-lanceolate branch leaves with slender, acuminate apices filled more or less with elongate apical cells. These collections, nevertheless, have short, oval to rhomboidal cells in the median region of the leaf concavity. A critical feature for recognizing *P. pycnothallodes* is the presence of the numerous rows of quadrate cells in the alar regions of the stipe and secondary stem leaves. Often the branch leaves also have many rows of quadrate alar cells, but this feature appears to be variably expressed in the branch leaves. Sporophytically, *P. pycnothallodes* is marked by its long-exserted, cylindrical capsules. The species also has large, cucullate calyptrae. When the smooth gemmae in *P. pycnothallodes* germinate, the new growth filaments are densely papillose and usually have shorter cells. This odd feature is found scattered throughout the Pterobryaceae, see, *e.g.*, *Pterobryopsis mexicana* and *Orthostichidium quadrangulare*.

Pireella crosbyi is very similar to *P. pycnothallodes*. Both species have erect-appressed stipe leaves, short, oval to rhomboidal cells in the median region of the leaf concavity, and alar cells strongly differentiated into numerous rows of quadrate cells. *Pireella crosbyi* differs from *P. pycnothallodes* in having rugose leaves, secondary stem leaves with partially recurved margins, and gemmae that are borne on the leaf apices.

Arzeni (1954) and Buck (1998) considered *P. pycnothallodes* closely related to *P. mariae*, because both species have erect-appressed stipe leaves, short, oval to rhomboidal cells in the median region of the leaf concavity, and exserted capsules. *Pireella mariae* differs from *P. pycnothallodes* in having stem leaves that are twice as large as the branch leaves and weakly to hardly differentiated alar cells. Arzeni (1954) also considered *P. pycnothallodes* to differ from *P. mariae* in having smooth setae, but in Central America the setae sometimes are scabrous. Buck (1998) considered *P. pycnothallodes* very close to *P. filicina*, which also has short branch leaf cells. *Pireella filicina* differs from

P. pycnothallodes in having squarrose stipe leaves and alar cells not or hardly differentiated, of only a few irregularly subquadrate, incrassate, porose cells at the basal angles.

In Central America *P. pycnothallodes* is more likely to be confused with *P. cymbifolia*, since both species have erect-appressed stipe leaves and leaves with numerous rows of quadrate alar cells. *Pireella cymbifolia* differs from *P. pycnothallodes* only in having weakly branched stems and elongate, sinuose cells in the median region of the leaf concavity.

7. *Pterobryon* Hornsch. *in* Mart., Fl. Bras. 1(2): 50. 1840. *Pilotrichum* sect. *Pterobryon* (Hornsch.) Müll. Hal., Syn. Musc. Frond. 2: 179. 1851 [*Pterobryum*].

Plants robust, in frondose masses on trees. Primary stems creeping, with small, erect to imbricate, distantly spaced leaves; rhizoids not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions and at base of secondary stems. Secondary stems irregularly spaced, erect, strongly stipitate, frondose to pinnately branched; stems in cross section with sclerodermis and enlarged thick-walled cortical cells, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous. Stipe leaves erect-appressed. Secondary stem leaves erect-spreading, lanceolate to ovate-lanceolate, acute to broadly acuminate, concave, plicate, shortly decurrent; margins serrate above, serrulate to subentire below, plane to somewhat incurved below; costae single, slender, occasionally spurred, ending below the apex; cells linear-flexuose, smooth, variably porose; alar cells weakly developed. Asexual reproduction by smooth, yellowish green to hyaline, uniseriate, septate gemmae arising from large, circular clusters of initials in leaf axils. Dioicous. Setae short. Capsules immersed, erect, symmetric, oval-oblong; stomata absent; opercula conic-rostrate; annuli complex; peristome diplolepideous; exostome teeth inserted within capsule mouth, linear-triangular, weakly trabeculate, prostome present; endostome rudimentary. Spores anisosporous. Calyptrae mitrate.

Pterobryon is a genus of eight species (Crosby *et al.* 2000) found in the Neotropics (3 species), Africa (2 species), China (1 species), Japan/Korea (1 species), and Australia (1 species). As characterized by Hornschuch (1840), the genus represents large, frondose, regularly, pinnately branched plants with immersed capsules and mitrate calyptrae. The type species (*P. densum*) also has plicate leaves, with long, single costae, smooth leaf cells, and weakly differentiated alar cells. Plicate leaves, however, are not found in any species outside the Neotropics. The genus is in need of critical revision, not only at the species level, but also at the generic level, because it is not at all clear how *Pterobryon* differs from *Pireella*. In the Neotropics *Pterobryon* is distinguished from *Pireella* by its more robust size and plicate, non-ranked leaves. Some *Pireella* species also differ from *Pterobryon* in having prorate leaf cells, well-developed alar cells, or short upper leaf cells.

The name *Pterobryon* combines the Greek *pteron* (feather) with *bryon* (moss). It was given to the genus by Hornschuch in reference to its "ramulos eleganter pinnatos."

Pterobryon densum Hornsch. *in* Mart., Fl. Bras. 1(2): 51. 1840. *Pilotrichum hornschuchii* Müll. Hal., Syn. Musc. Frond. 2: 179. 1851, new name, not *Pilotrichum densum* (Hedw.) Müll. Hal., Syn. Musc. Frond. 2: 160. 1850. Protologue. [Brazil] In cortice arborum, loco natali non indicato: *Sellow*.

Cryptotheca densa Hornsch. *ex* Schltdl. & Cham., Linnaea 6: 62. 1831, invalid name, lacks a description. Based on: Prope Jalapam et Mexico, [*Schiede & Deppe*] *N° 1084*.

Cryptotheca densa Hornsch. *in* Mart., Fl. Bras. 1(2): 51. 1840, invalid name, listed in synonymy.

Porotrichum plumosum Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32(1): 191. 1894. Protologue. [Costa Rica] Forêts du Río Naranjo, 200–250 m (*Pitt*[*ier*] *n° 5710*). Type. Plantae costaricenses exsiccatae *N° 5710.* Forêts du Río Naranjo. Mars 1893, legit (*H. Pittier*) *Tonduz* [Herb. J. Cardot] (PC, holotype).

Prionodon splendens Herzog, Beih. Bot. Centralbl. 26(2): 77. 1909. Protologue. Bolivia: An Bäumen im Bergurwalde bei Incacorral (Prov. Cochabamba), ca. 2200 m; Januar, 08 [*Herzog 5035*].

Pterobryon densum var. *peracuminatum* Cardot, Rev. Bryol. 37: 7. 1910 [*Pterobryum*]. Protologue. [Mexico] État de Hidalgo: Honey-station, 1904 (*Pringle, n. 15070*).

Pterobryon panamense Cardot & Thér. *in* Thér., Bull. Acad. Int. Géogr. Bot. 21: 271. 1911 [*Pterobryum*]. Protologue. Panama, leg *f^re^ Hélion*. Type. Panama, leg. *fre. Helion* (FH, isotype).

Pterobryon densum var. *condensatum* Lorentz *ex* Arzeni, Amer. Midl. Naturalist 52: 21. 1954, invalid name, listed in synonymy.

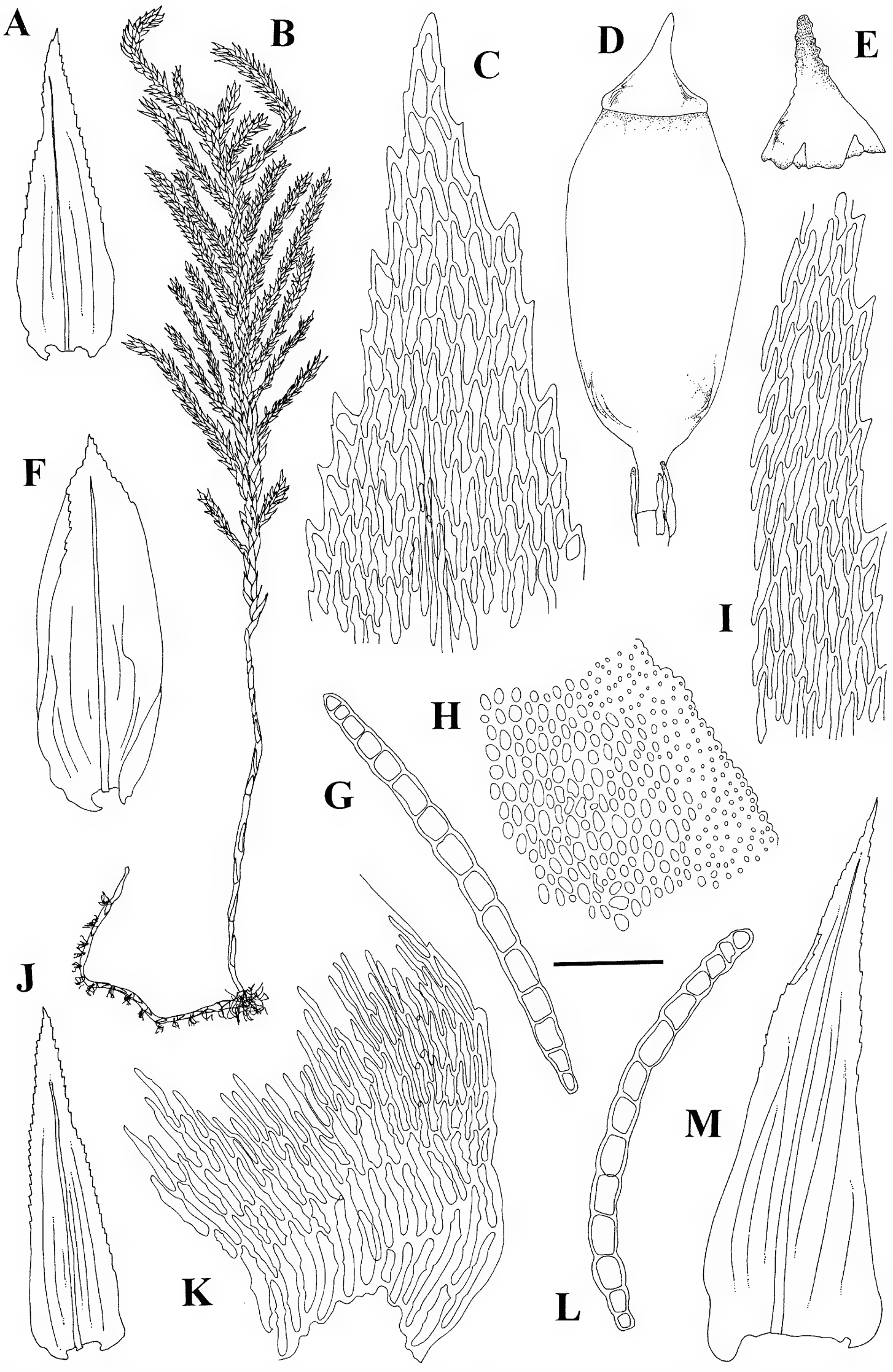


Figure 79. *Pterobryon densum*. A & J. Branch leaves. B. Habit. C. Leaf apex. D. Seta, capsule, and operculum. E. Calyptra. F. Branch leaf from *panamense* expression. G & L. Gemmae. H. Stem in cross section. I. Median leaf cells and margin. K. Basal and alar cells. M. Stem leaf. Scale in mm: bar = 0.06 (C, I, K); bar = 0.08 (H); bar = 0.13 (G, L); bar = 0.6 (D, E); bar = 0.7 (A, F, J, M); bar = 10.1 (B). F from *Dauphin 1501*; G & L from *Croat 13751D*; all other figure parts from *Allen 12157*.

Pterobryaceae

Plants robust, in dark green, dense, frondose masses on trees. Primary stems creeping, with small, erect to imbricate, distantly spaced leaves; rhizoids red brown, smooth to roughened, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions and at base of secondary stems. Secondary stems irregularly spaced, erect, strongly stipitate, frondose to pinnately branched, to 13 cm long; stems in cross section with sclerodermis of 5–8 rows of small, red to reddish yellow, thick-walled cells, cortical cells enlarged, yellow, thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous. Stipe leaves erect-appressed, oblong-lanceolate, to 3 mm long. Secondary stem leaves erect-spreading, 2.5–4.0 mm long, lanceolate to ovate-lanceolate, acute to broadly acuminate, concave, plicate, shortly decurrent; margins serrate above, serrulate to subentire below, plane to somewhat incurved below; costae single, slender, occasionally spurred, ending below the apex; cells linear-flexuose, smooth, variably porose, firm-walled throughout, apical cells 14–40 × 5–10 μm, median cells 30–65 × 4–8 μm; alar cells weakly developed, of a few irregularly subquadrate, incrassate, porose cells at the basal angles, cells across the insertions yellow. Branch leaves lanceolate, 1.5–2.5 mm long, broadly acuminate, weakly concave, plicate; upper margins strongly serrate. Asexual reproduction by smooth, yellowish green to hyaline, uniseriate, septate gemmae arising from large, circular clusters of initials in leaf axils. Dioicous. Perigonia lateral on upper secondary stems and branches. Perichaetia large, leaves oblong-lanceolate, 4–5 mm long. Setae short, smooth, reddish, 0.5 mm long. Capsules immersed, erect, symmetric, oval-oblong, 1.2–2.0 mm long; exothecial cells at mouth small and reddish, lower cells short-rectangular, rounded-quadrate to oblate, firm-walled; stomata absent; opercula conic-rostrate, 1.0 mm long; annuli complex, of several rows of thin-walled, papillose-roughened outer cells and 1–2 rows of enlarged, rounded, very thick-walled interior cells usually clinging to operculum on dehiscence; peristome diplolepideous; exostome teeth deeply inserted within capsule mouth, pale yellow, linear-triangular, to 450 μm, smooth, weakly trabeculate, prostome present; endostome rudimentary. Spores round to oblong, smooth to lightly papillose, anisosporous, 12–16 μm (seemingly aborted) and 40–60 μm. Calyptrae mitrate, 1 mm long, roughened above, naked.

Illustrations. Brotherus (1925, Fig. 549); Bartram (1949, Fig. 116 E–G); Arzeni (1954, Pls. 11–13); Sharp *et al.* (1994, Fig. 528); Churchill and Linares (1995, Fig. 168 a–e); Buck (1998, Pl. 51); Gradstein *et al.* (2001, Fig. 196 A–E). Figure 79.

Habitat. On vertical tree trunks, roots, branches, and vines, rarely on rocks; 140–2500 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: *Türckheim 7769* (NY); Chimatenango: *Godman & Salvin* (NY); Quetzaltenango: *Standley 67886* (F, FH); San Marcos: *Steyermark 36485* (F, FH); Sololá: *Steyermark 47356* (F, FH); Suchitepéquez: *Steyermark 46661* (F, FH, MO, NY, US). EL SALVADOR. Chalatenango: *Sipman et al. 37641* (NY); Santa Ana: *Watson ES-0072* (MO). HONDURAS. Francisco Morazán: *Richards et al. 3655* (F); Lempira: *Allen 11351A* (MO, TEFH); Ocotepeque: *Allen 14485* (MO, TEFH); Olancho: *Allen 12532* (MO, TEFH). NICARAGUA. Granada: *Moreno & Henrich 8535* (MO). COSTA RICA. Alajuela: *Standley & Torres 47594* (FH, NY, US); Cartago: *Standley 34500* (FH, NY, US); Guanacaste: *Crosby 3856* (MO, NY); Heredia: *Crosby 10864* (BM, CR, DUKE, F, FH, H, MO, NY, US); Limón: *Gutiérrez 188* (F, FH, NY); Puntarenas: *Gómez et al. 21698* (MO); San José: *Standley 41923* (FH, NY, US). PANAMA. Bocas del Toro: *Allen 5860* (MO); Chiriquí: *Allen 5411* (MO); Veraguas: *Crosby 10258* (MO, PMA).

World range: Mexico; Central America; Caribbean; Western and Northern South America, Brazil.

Pterobryon densum is a robust, frondose species nearly always found epiphytic on tree trunks. Typically the species has narrow, weakly concave, strongly plicate, ovate-lanceolate, and toothed leaves. There is, however, a fairly common form in Central America with broad, strongly concave, weakly plicate, oblong, and broadly acute leaves. This odd form was described as *Pterobryon panamense*, but in many collections of the *panamense*-form typical plants of *P. densum* can also be found. More importantly, some collections (including the type of *P. panamense*) have plants with leaves on the lower parts that resemble the *panamense*-form, but on the upper parts have typical features. Although *P. densum* is dioicous, it often has immersed capsules with mitrate calyptrae. Arzeni (1954) reported "polymorphous" spores in this species, and the spores of *P. densum* are 2-sized, but the smaller ones appear to be non-viable.

Prionodon is sometimes confused with *Pterobryon densum* because both are large, epiphytic, often highly branched taxa with similar leaf shapes. *Prionodon* differs from *P. densum* in lacking stipitate secondary stems and in having shorter, often collenchymatous, papillose leaf cells. *Pterobryon densum* differs from all Central American species of *Pireella* in its robust size and strongly plicate leaves. In addition, some species of *Pireella* differ from *Pterobryon densum* in having ranked leaves and papillose leaf cells.

Although the protologue of *Porotrichum plumosum* appears to indicate Pittier collected the material, the type collection was actually made by Tonduz. The protologue citation "(*Pitt. n° 5710*)" refers to its number in H. Pittier and Th. Durand's *Plantae costaricenses exsiccatae*.

8. *Pterobryopsis* M. Fleisch., Hedwigia 45: 56. 1906.

Pterobryopsis sect. *Eupterobryopsis* M. Fleisch., Hedwigia 45: 57. 1905, illegitimate name.
Pterobryopsis sect. *Pterobryodendron* M. Fleisch., Hedwigia 45: 59. 1905.

Plants medium-sized to robust, in yellow green, loose or dense mats. Primary stems creeping with small, imbricate-appressed, distantly spaced leaves; rhizoids red brown, smooth, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions, and at base of stipes. Secondary stems irregularly spaced, erect and stipitate, with evenly foliate stipe leaves or pendent, not to sparsely branched or irregularly pinnate-branched, branches at times becoming flagellate; stems in cross section with sclerodermis, enlarged, firm-walled cortical cells, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous. Secondary stem leaves acute to acuminate, apices cucullate or plane, concave, rounded at base or auriculate, decurrent; margins entire below, serrulate to denticulate above, plane; ecostate or costae short and double or single and slender ending at or somewhat above midleaf, in cross section cells homogeneously thick-walled; cells linear-flexuose, smooth, often porose and firm-walled throughout, cells across the insertions yellowish red; alar cells well developed. Asexual gemmae often present, from circular clusters of initials in leaf axils, cylindrical, uniseriate but occasionally biseriate at the tips, gemmae becoming secondarily elongate, cells smaller, at times papillose-roughened. Setae smooth, short or long. Capsules immersed or shortly exserted, oblong to ovate-cylindrical; exothecial cells hexagonal to short-rectangular; stomata phaneroporic; opercula conic or short-rostrate; annuli rudimentary; peristome diplolepideous, exostome smooth, yellow to hyaline, prostome present or absent; endostome absent or rudimentary and consisting of only a short basal membrane. Spores large, lightly papillose. Calyptrae smooth, cucullate or mitrate.

Pterobryopsis is a genus of 29 species (Crosby *et al.* 2000) found mostly in India and Southeast Asia. The genus has plants with distinctly creeping primary stems, and nearly all its species have strongly stipitate secondary stems. There are, however, some species of *Pterobryopsis* with pendent stems. The secondary stems vary from unbranched to irregularly pinnately branched, with nonranked, often tumid leaves. The leaves have well-developed alar cells and costae that vary from absent to short-double or long-single. The median leaf cells are long, firm- to thick-walled, and often porose. The sporophytes of many species are unknown. Those with sporophytes can have long or short setae and exserted or immersed capsules. The peristome is diplolepideous, with smooth exostome teeth that often have prostome development, and absent or rudimentary endostomes. When rudimentary, the endostome consists only of a very short basal membrane. The calyptrae can be cucullate or mitrate.

In view of the remarkable morphological variation noted above, it is not surprising that *Pterobryopsis* has been considered a heterogeneous "conglomerate" grouping (Magill 1983) in need of revision. Indeed, as presently circumscribed, the genus *Pterobryopsis* is impossible to cleanly separate from *Jaegerina*, *Renauldia*, and *Calyptothecium*. The separation of *Pterobryopsis* from *Calyptothecium* is especially problematic, as can be seen by comparing the African treatments by Argent (1973a) and Magill and Rooy (1998): species treated by the former in *Calyptothecium* were placed in *Pterobryopsis* by the latter.

In Central America there is only one species of *Pterobryopsis*, and this makes recognition of the genus much easier. In a regional sense, *Renauldia* differs from *Pterobryopsis* in having leaves that are

ecostate or have short double costae and weakly developed alar cells. *Jaegerina* differs from *Pterobryopsis* in having unbranched or weakly branched secondary stems and leaves with weakly developed alar cells. *Calyptothecium* differs from *Pterobryopsis* in having complanate leaves that are rounded to auriculate at base and have weakly developed alar cells. There are, however, some forms of *Calyptothecium* in Central America that have turgid leaves.

The name *Pterobryopsis* combines the generic name *Pterobryon* with the Greek *opsis* (indicating appearance or resemblance).

Pterobryopsis mexicana (Renauld & Cardot) M. Fleisch., Hedwigia 45: 56. 1905. *Garovaglia mexicana* Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 38(1): 18. 1899. Protologue. Mexique (herb. Röll).

Cryptotheca mexicana Schimp. *in* Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 38(1): 18. 1899, invalid name, listed in synonymy.

Pterobryopsis subfrondosa M. Fleisch., Hedwigia 45: 60. 1905, invalid name, lacks a description. *Climaciella subfrondosa* Müll. Hal. *in* M. Fleisch., Hedwigia 45: 60. 1905, invalid name, lacks a description.

Pterobryopsis pringlei Cardot, Rev. Bryol. 37: 8. 1910. Protologue. [Mexico] État de Vera Cruz: près de Jalapa, 1908 (*Pringle, n. 15150 in parte*).

Plants medium-sized to robust, in yellow green, loose or dense mats. Primary stems creeping, with small, imbricate-appressed, distantly spaced, ecostate, lanceolate leaves, 0.4–0.8 mm long; rhizoids red brown, smooth, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions, and at base of stipes. Secondary stems irregularly spaced, erect and stipitate, with evenly foliate stipe leaves or pendent, irregularly pinnate-branched, branches at times becoming flagellate, 4–10 cm long; stems in cross section with sclerodermis of 4–8 rows of small, reddish yellow, thick-walled cells, cortical cells enlarged, yellowish to hyaline, firm- to thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous. Secondary stem leaves tumid to laxly imbricate, at times loosely spreading, 2.0–3.5 mm long, ovate, shortly acute, concave, rounded at base, strongly decurrent; margins entire below, serrulate to denticulate above, plane; costae single, slender, ending at or somewhat above midleaf, in cross section cells homogeneously thick-walled; cells linear-flexuose, smooth, porose and firm-walled throughout, apical cells 14–48 × 4–10 μm, median cells 28–64 × 4–10 μm; basal cells 40–90 × 6 μm, cells across the insertions yellowish red; alar cells very well developed, quadrate to oblate in 10–30 rows, incrassate, 9–24 × 9–22 μm. Branch leaves somewhat smaller (1.5–3.0 mm long) than the secondary stem leaves, but otherwise similar. Asexual gemmae common, from circular clusters of initials in leaf axils, cylindrical, uniseriate, but occasionally biseriate at the tips, 3–12 cells long, gemmae becoming secondarily elongate, cells smaller and papillose-roughened. Sporophyte unknown.

Illustrations. Bartram (1949, Fig. 113 A–C); Arzeni (1954, Pls. 9 & 10); Sharp *et al.* (1994, Fig. 529); Gradstein *et al.* (2001, Fig. 196 F–K). Figure 80.

Habitat. On tree trunks and rotting logs, occasionally on boulders; 1050–2000 m.

Distribution in Central America. GUATEMALA. Baja Verapaz: *Sharp 2885* (FH, US); Chimaltenango: *Standley 81074a* (F, FH); Jalapa: *Standley 77500a* (F, FH); Sacatepéquez: *Standley 63730* (F, FH). EL SALVADOR. Cuscatlán: *Calderón 1996 p.p.* [filed under *Pireella pohlii*] (NY, US). HONDURAS. Comayagua: *Allen 13739* (MO). NICARAGUA. Jinotega: *Standley 11066* (F, FH); Matagalpa: *D'Arcy s.n.* (F, MO). COSTA RICA. Heredia: *Valerio 105* (FH, US); San José: *Griffin & Morales B 98* (F, MO, NY). PANAMA. Chiriquí: *Crosby 3963* (MO).

World range: Mexico; Central America.

Pterobryopsis mexicana is a medium-sized to robust species that has distinctly frondose/stipitate plants. Its leaves are evenly foliate and typically imbricate-appressed to somewhat spreading when dry. Distinctive microscopical features of *P. mexicana* leaves include their long decurrencies, slender costae that end at or above midleaf, and extensively developed, quadrate to oblate alar cells that sometimes occur in as many as 30 rows. Plants of *P. mexicana* nearly always have numerous short, cylindrical, uniseriate gemmae that arise from circular clusters of initials in the leaf axils. The gemmae are smooth and sometimes clavate in shape, but after detaching they elongate at one end and the new cells

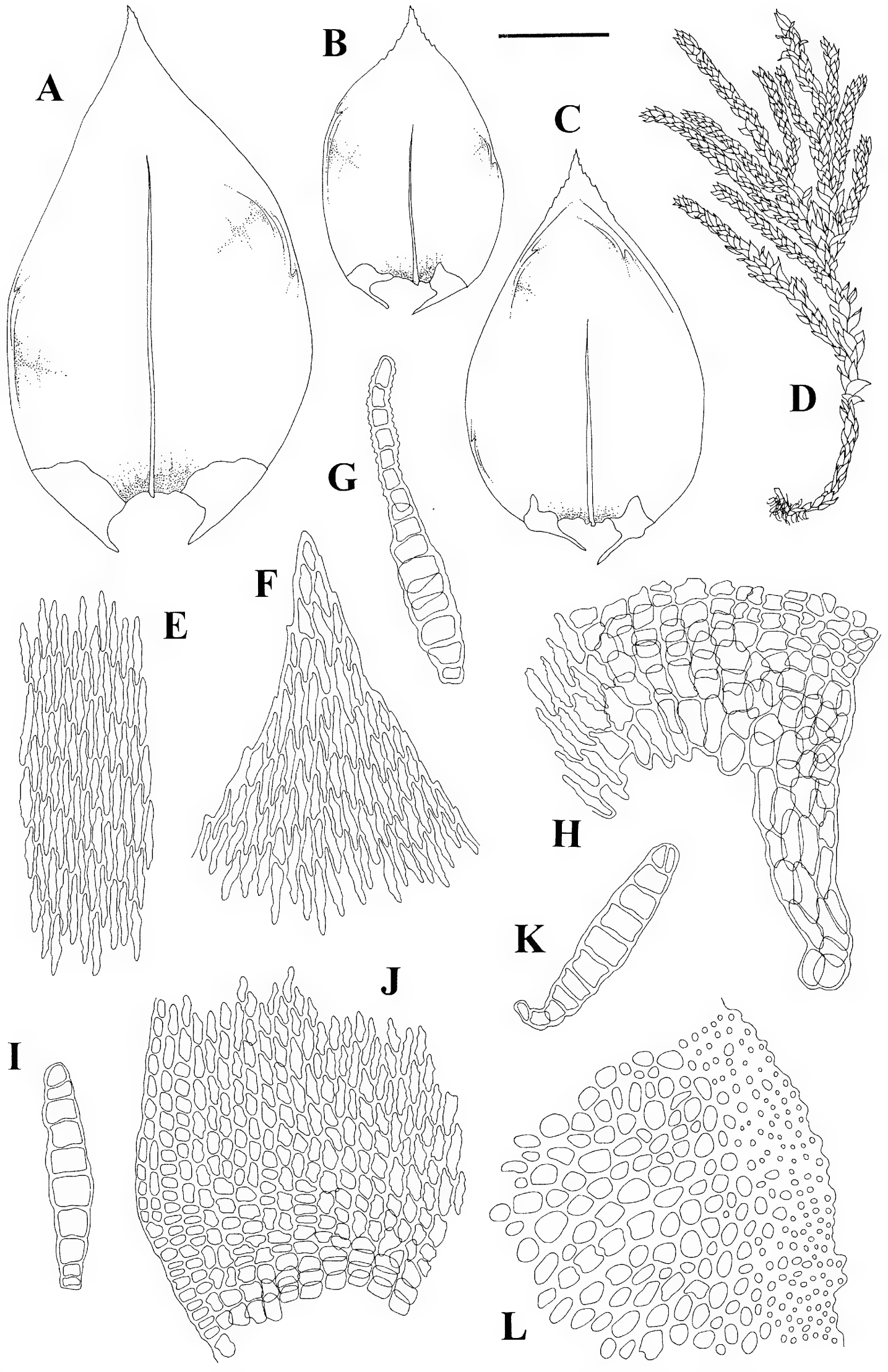
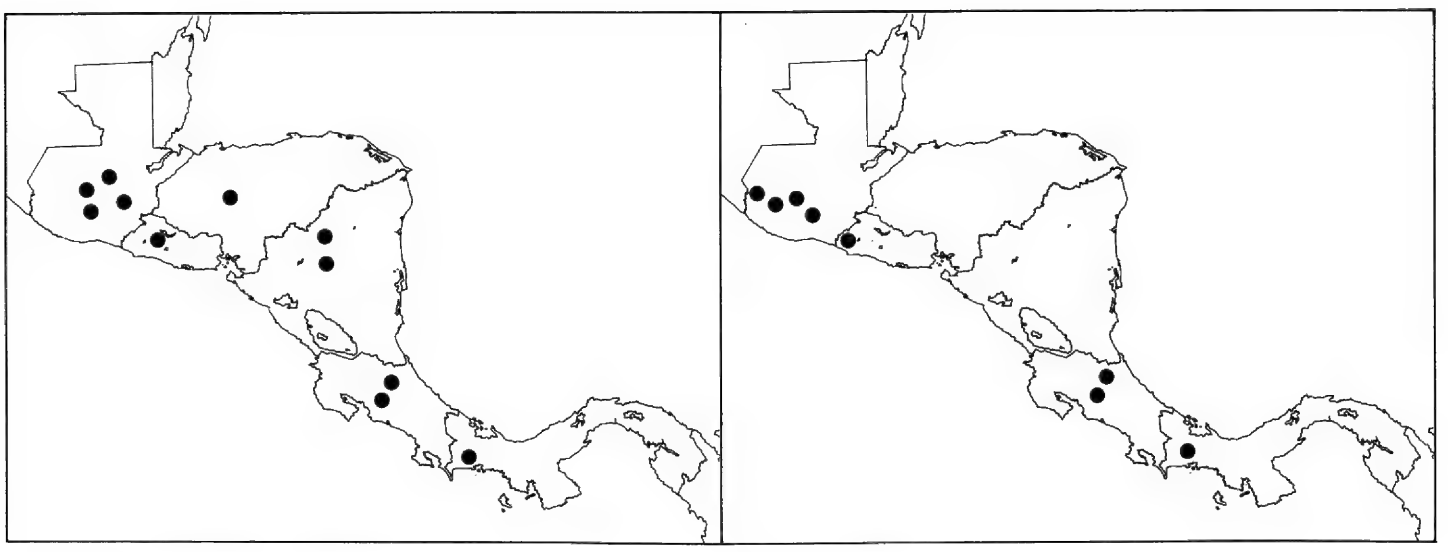


Figure 80. *Pterobryopsis mexicana*. A. Stem leaf. B & C. Branch leaves. D. Habit. E. Median leaf cells. F. Leaf apex. G, I & K. Gemmae. H & J. Basal and alar cells. L. Stem in cross section. Scale in mm: bar = 0.08 (E–L); bar = 0.6 (A–C); bar = 8.0 (D). All figure parts from *Allen 13739*.



Pterobryopsis mexicana *Renauldia mexicana*

are commonly papillose-roughened. This gemma feature is also seen in *Orthostichidium quadrangulare* and *Pireella pycnothallodes.*

As noted by Arzeni (1954), plants of *P. mexicana* can be variable in aspect and relative size. This variation falls within two main forms. One form consists of robust plants that have strongly stipitate stems, with distinctly differentiated stipe leaves, and somewhat spreading branch leaves. The second form is often medium in size. It has weakly stipitate stems, with stipe and upper secondary stem leaves more or less similar, and its branch leaves are often imbricate-appressed. The second Central American form of *P. mexicana* appears gametophytically identical to the South American *Pterobryopsis stolonacea* (Müll. Hal.) Broth. The name *P. stolonacea* predates *P. mexicana* by 21 years, but having not examined the type of *P. stolonacea*, I have not synonymized the two taxa.

The non-ranked, imbricate-appressed leaves of *P. mexicana* give it an appearance somewhat similar to *Renauldia mexicana.* That species differs from *P. mexicana* in having ecostate leaves and weakly differentiated alar cells. Plants of *Orthostichidium quadrangulare* are similar in size to those of *P. mexicana*, and their leaves are similar in shape. The leaves of *O. quadrangulare* (especially when wet) differ from those of *P. mexicana* in occurring in distinct spiral rows, they are ecostate, and they have weakly differentiated alar cells. *Jaegerina scariosa* could be confused with *P. mexicana*, because that species has non-ranked, concave leaves that are similar in shape to those of *P. mexicana.* However, *J. scariosa* is a much smaller plant than *P. mexicana*, with simple or sparsely branched stems, and squarrose to wide-spreading leaves. The leaves of *J. scariosa* also have considerably less developed alar cells than those of *P. mexicana.*

9. *Renauldia* Müll. Hal. *in* Renauld, Rev. Bot. Bull. Mens. 9: 221. 1891.

Plants medium-sized to robust, in green to yellow green, loose or dense mats, at times pendent. Primary stems creeping, with erect to imbricate, distantly spaced leaves; rhizoids red brown, smooth, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions and at base of stipes. Secondary stems irregularly spaced, erect, stipitate, irregularly branched; stems in cross section with sclerodermis, enlarged, firm-walled cortical cells, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous. Primary stem leaves erect-appressed, ovate, ovate-triangular, narrowly acuminate; costae short and double or absent. Secondary stem and branch leaves erect-spreading to imbricate, obovate, oblong-ovate, deeply concave, at times rugose, broadly acute or long, narrowly acuminate, rounded to the insertion or auriculate, not or weakly decurrent; margins entire throughout or serrulate above, erect to incurved; costae short and double or absent; cells linear-flexuose, firm-walled, often porose; alar cells weakly developed, rhombic to short-rectangular or sharply differentiated in small, excavate groups, cells across the leaf base orange red, thick-walled. Dioicous. Setae short, smooth. Capsules immersed, erect, symmetric, oval to oblong; exothecial cells short-rectangular to subquadrate, firm-walled; stomata absent; opercula conic-rostate; annuli large,

complex, revoluble; peristome diplolepideous, prostome well developed; exostome teeth yellow, narrowly triangular, smooth to finely roughened, weakly trabeculate; endostome absent or a rudimentary hyaline membrane fused to the exostome. Spores irregularly rounded, oval, or oblong, smooth to lightly roughened, large (to 60 μm long). Calyptrae mitrate, but with one side split considerably more than the others, smooth, naked.

Renauldia is a genus of nine species (Crosby *et al.* 2000) found in Africa and Central/South America. The genus has evenly foliate stems with unranked, ecostate leaves that are rounded or auriculate at base and have poorly developed alar cells. The capsules of *Renauldia* are immersed and they lack stomata. Its diplolepideous peristome has a well-developed prostome, and the exostome teeth are irregularly developed. The endostome is absent or rudimentary and present as a short hyaline membrane fused to the exostome teeth. Although the calyptrae of *Renauldia* are technically mitrate, they are split considerably longer on one side than on the others in the same manner as often occurs in *Schistidium.*

When considered overall, the genus is difficult to separate from *Hildebrantiella*, *Calyptothecium*, *Orthostichidium*, and *Pterobryopsis*. Typically, *Hildebrantiella* differs from *Renauldia* in having numerous inflated alar cells and strongly decurrent leaves. Although *Calyptothecium* is usually distinguished from *Renauldia* by its complanate or flattened leaves, all species of *Calyptothecium* have turgid, non-complanate forms. *Orthostichidium* mostly differs from *Renauldia* in having strongly ranked leaves, but there are some species of *Orthostichidium* with unranked leaves. *Pterobryopsis* typically differs from *Renauldia* in having single costate leaves; however, there are ecostate species of *Pterobryopsis*. All five genera are in need of revision. Argent (1973a, 1973b) provided a detailed treatment of these genera in Africa.

The name *Renauldia* is given in honor of Ferdinand [François Gabriel] Renauld (18 November 1837–6 May 1910). Renauld was a French soldier (8 campaigns in Algeria) and later Commandant of the Palace of Monaco. He was awarded the Légion d'honneur in 1884 (Stafleu & Cowan 1983). Renauld published papers on the bryology of France, North America, Costa Rica, and Africa (especially Madagascar). During his productive 25-year collaboration with Jules Cardot they described seven genera and more than 400 species (Thériot 1910).

1. Leaves broadly acute, rounded to the insertions; alar cells weakly differentiated . . . . . 1. *R. mexicana*
1. Leaves long, narrowly acuminate, auriculate at base; alar cells sharply differentiated . . . . . 2. *R. paradoxica*

1. *Renauldia mexicana* (Mitt.) H. A. Crum *in* H. A. Crum & Arzeni, Rev. Bryol. Lichénol. 22: 154. 1953. *Meteorium mexicanum* Mitt., J. Linn. Soc., Bot. 12: 433. 1869. Protologue. Mexico, *Deppe et Schiede*; Cordillera de Oaxaca, *Galeotti, n. 6886.*

Cryptotheca cochlearifolia Hornsch. *ex* Schltdl. & Cham., Linnaea 6: 62. 1831, invalid name, lacks a description. *Renauldia cochlearifolia* (Hornsch.) Broth., Nat. Pflanzenfam. (ed. 2) 11: 146. 1925. Based on: Prope urbem Mexico, [*Schiede & Deppe*] *N°. 1083.*

Pilotrichum cochlearifolium Müll. Hal., Syn. Musc. Frond. 2: 182. 1851, illegitimate homonym, not *Pilotrichum cochlearifolium* Müll. Hal., 1843. *Pterobryum cochlearifolium* A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 238. 1877, new name for *Pilotrichum cochlearifolium* Müll. Hal., 1851. Protologue. Mexico: *Deppe et Schiede.*

Plants medium-sized to robust, in green to yellow green, loose or dense mats. Primary stems creeping with erect to imbricate, distantly spaced leaves; rhizoids red brown, smooth, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions and at base of stipes. Secondary stems irregularly spaced, erect, stipitate, irregularly pinnately branched, 3–10 cm long; stems in cross section with sclerodermis of 5–8 rows of small, reddish yellow, thick-walled cells, cortical cells enlarged, yellowish to hyaline, firm- to thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous. Stipe leaves erect-appressed, ovate-triangular, 1.4–2.0 mm long, acuminate, shortly decurrent; costae short and double. Secondary stem and branch leaves closely spaced, erect to imbricate, 2.5–4.0 mm long, oblong-ovate, deeply concave, rugose, broadly acute, rounded to the insertion, weakly decurrent; margins entire throughout or serrulate above, erect to in-

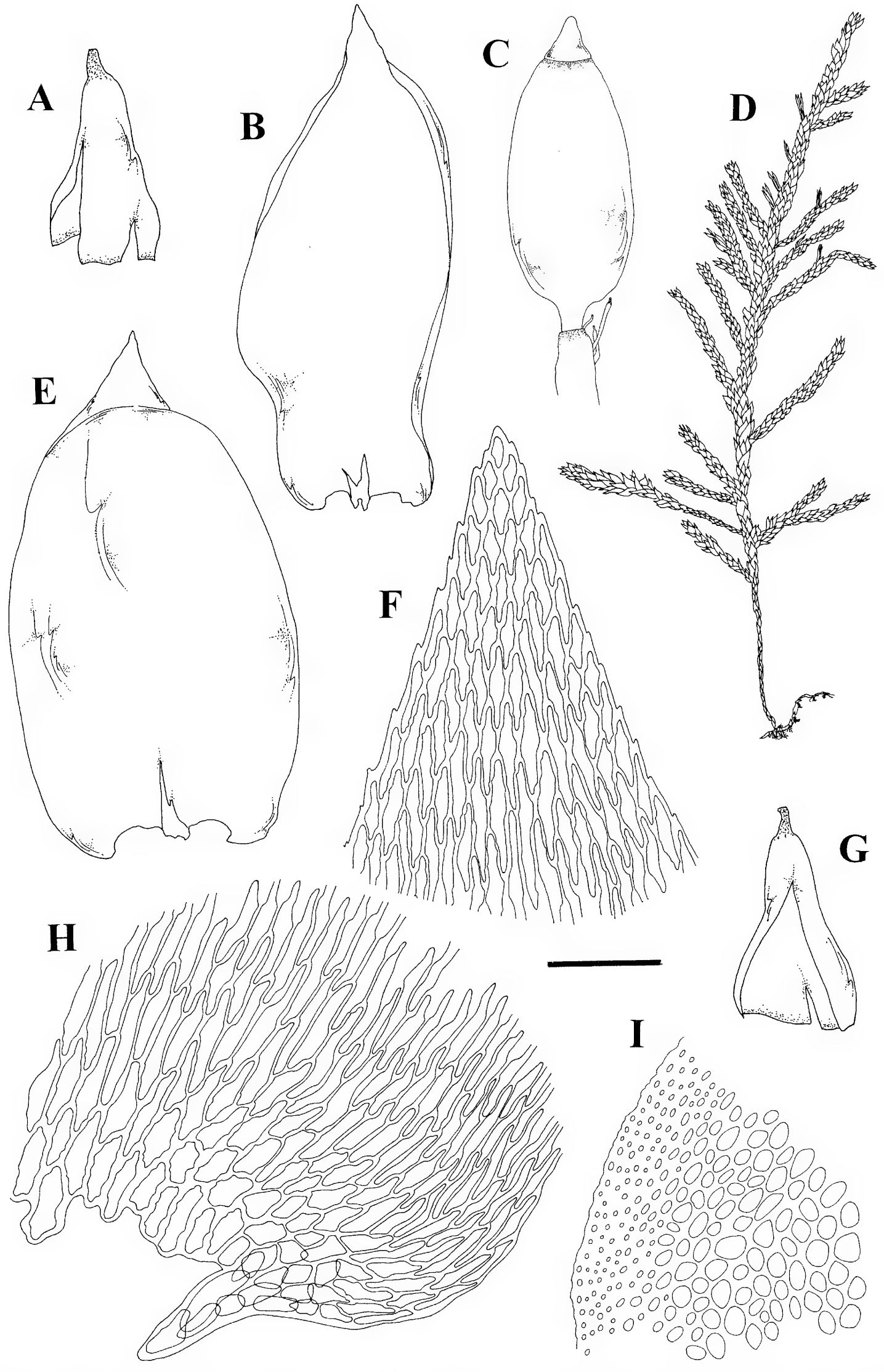


Figure 81. *Renauldia mexicana*. A & G. Calyptrae. B & E. Leaves. C. Seta, capsule, and operculum. D. Habit. F. Leaf apex. H. Basal and alar cells. I. Stem in cross section. Scale in mm: bar = 0.06 (F, H); bar = 0.08 (I); bar = 0.4 (A, G); bar = 0.5 (B, E); bar = 0.8 (C); bar = 12.7 (D). A, C, G from *Pringle 10658*; all other figure parts from *Crosby 9913*.

curved; costae short and double or sometimes absent; cells linear-flexuose, firm-walled, often porose, apical cells 40–90 × 4–8 μm, median cells 50–110 × 4–6 μm; basal cells 24–70 × 6–22 μm; alar cells very weakly developed, rhombic to short-rectangular, in 2 rows. Dioicous. Perichaetia lateral along stems and branches, to 4.0 mm long; leaves ovate-lanceolate, ecostate, to 1.5 mm long. Setae short, smooth, 0.2–0.5 mm long, Capsules immersed, erect, symmetric, oval to oblong, 1.5–2.0 mm long; exothecial cells short-rectangular to subquadrate, firm-walled; stomata absent; opercula conic-rostrate, 0.4–0.5 mm long; annuli large, complex, revoluble; peristome diplolepideous, prostome well developed; exostome teeth yellow, narrowly triangular, smooth to finely roughened, weakly trabeculate; endostome apparently absent. Spores irregularly rounded, oval, or oblong, smooth to lightly roughened, 22–60 μm long. Calyptrae mitrate, but with one side split considerably more than the others, smooth, naked, 0.8 mm long.

Illustrations. Bartram (1949, Fig. 113 D–E); Arzeni (1954, Pls. 5 & 6); Sharp *et al.* (1994, Fig. 526); Gradstein *et al.* (2001, Fig. 196 L–R). Figure 81.

Habitat. On bark of trees and rotting vines; 1600–3048 m.

Distribution in Central America. GUATEMALA. Chimaltenango: *Standley 80167a* (F, FH); Quetzaltenango: *Steyermark 33941* (F, FH); Sacatepéquez: *Standley 63711b* (F, FH); San Marcos: *Sharp* 5469 (F, FH, MO). EL SALVADOR. Ahuachapán: *Davidse et al. 37471* (MO). COSTA RICA. Heredia: *Crosby 9913* (MO); San José: *Holz CR 00-0431* (MO). PANAMA. Chiriquí: *McPherson 9307D* (MO).

World range: Mexico; Central America.

Renauldia mexicana is a high elevation, medium-sized to robust species with stipitate, irregularly pinnately branched stems. It has non-ranked, strongly concave to tumid leaves, with short, double or absent costae and very weakly differentiated alar cells. Unlike many other species in the Pterobryaceae, *R. mexicana* seems to lack clusters of uniseriate gemmae in its leaf axils. The peristome of *R. mexicana* is very irregular. Although it has a clearly differentiated prostome, the endostome appears to be either absent or reduced to a hyaline membrane that is fused to the back of the exostome. The annulus of *R. mexicana* is revoluble and complex. It consists of three or four layers of enlarged, differentiated cells, often with one of the layers remaining attached to the operculum after capsule dehiscence.

The non-ranked, tumid leaves of *R. mexicana* give it an appearance very similar to *Pterobryopsis mexicana.* That species differs from *R. mexicana* in having long, single costae and well-differentiated alar cells. *Orthostichidium quadrangulare* resembles *R. mexicana* in size, plant aspect, in having leaves that are rounded to the insertion, short, double or absent costae, and very weakly developed alar cells. The leaves of *O. quadrangulare*, however, are (especially when wet) in distinct spiral rows, and they are narrower (especially at the apex) than those of *R. mexicana*. Furthermore, plants of *O. quadrangulare* nearly always have abundant gemmae in their leaf axils. *Jaegerina scariosa* has sometimes been confused with *R. mexicana*, because that species has non-ranked concave leaves that sometimes have short, double or even absent costae. Nevertheless, *J. scariosa* is a much smaller plant than *R. mexicana*, with simple or sparsely branched stems, and squarrose to wide-spreading leaves. The leaves of *J. scariosa* are broadly ovate, and at least some leaves can usually be found with long single costae.

2. *Renauldia paradoxica* B. H. Allen, J. Bryol. 14: 678. 1987. Protologue. Panamá. Veraguas Prov.: Stream valley 10.4 km along road leading NW from Escuela Agricola 'Alto de Piedra,' 5.4 km NW of Sante Fé, elev. 350 m, 8°30′N; 81°05′W. 16 May 1975. *Crosby 10154*. Types. Panama. Prov. Veraguas. Stream valley 10.4 km along road leading NW from Escuela Agricola "Alto de Piedra," 5.4 km NW of Sante Fé. Alt. 350 m, 8°30′N; 81°05′W. 16 May 1975. *Crosby 10154* (MO, holotype; PMA, isotype).

Plants medium-sized, in green to yellow green, loose mats, often pendent. Primary stems creeping, with erect to imbricate, distantly spaced leaves; rhizoids red brown, smooth, not or irregularly branched, from clusters of initials at abaxial side of primary stem leaf insertions and at base of stipes.

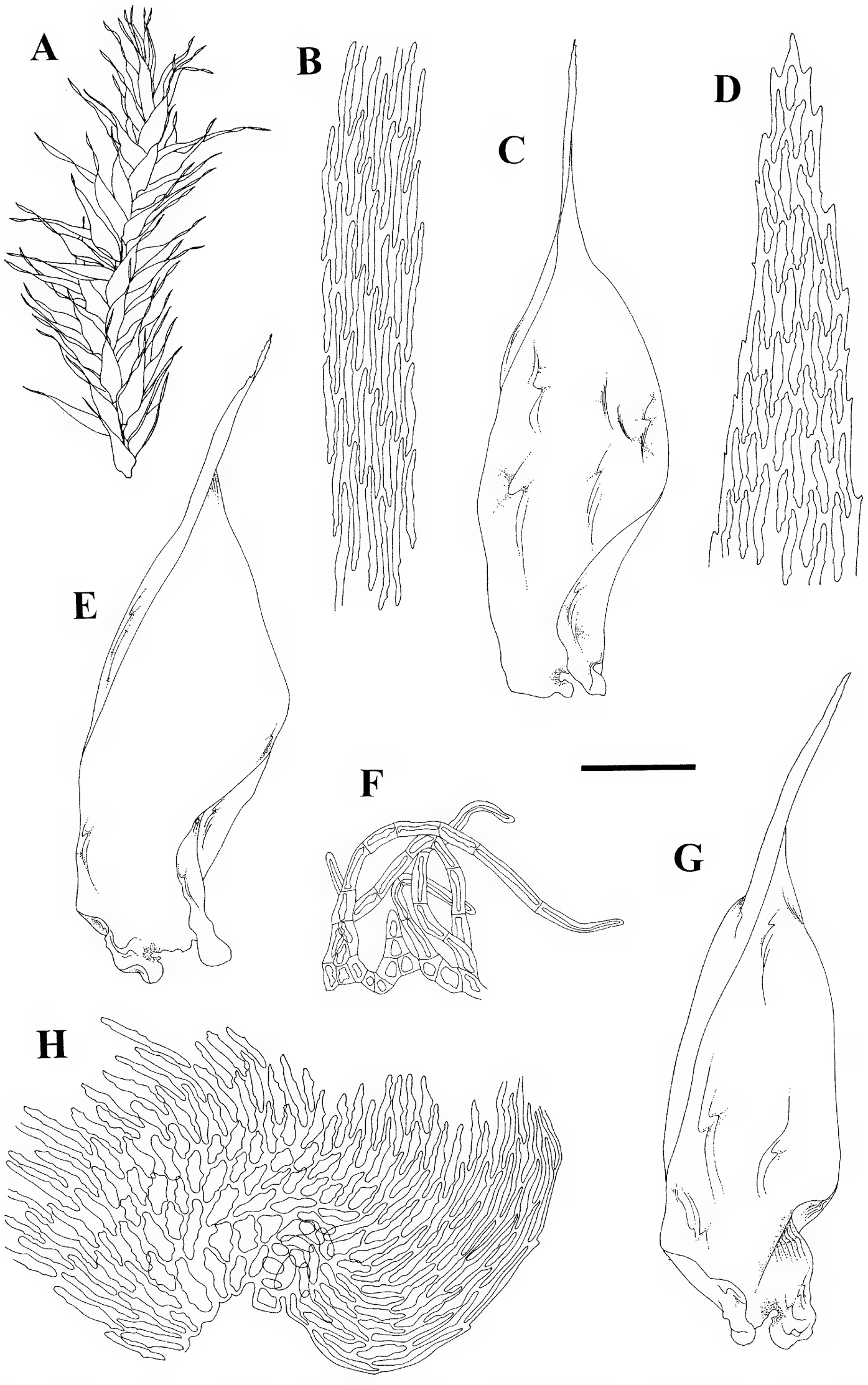
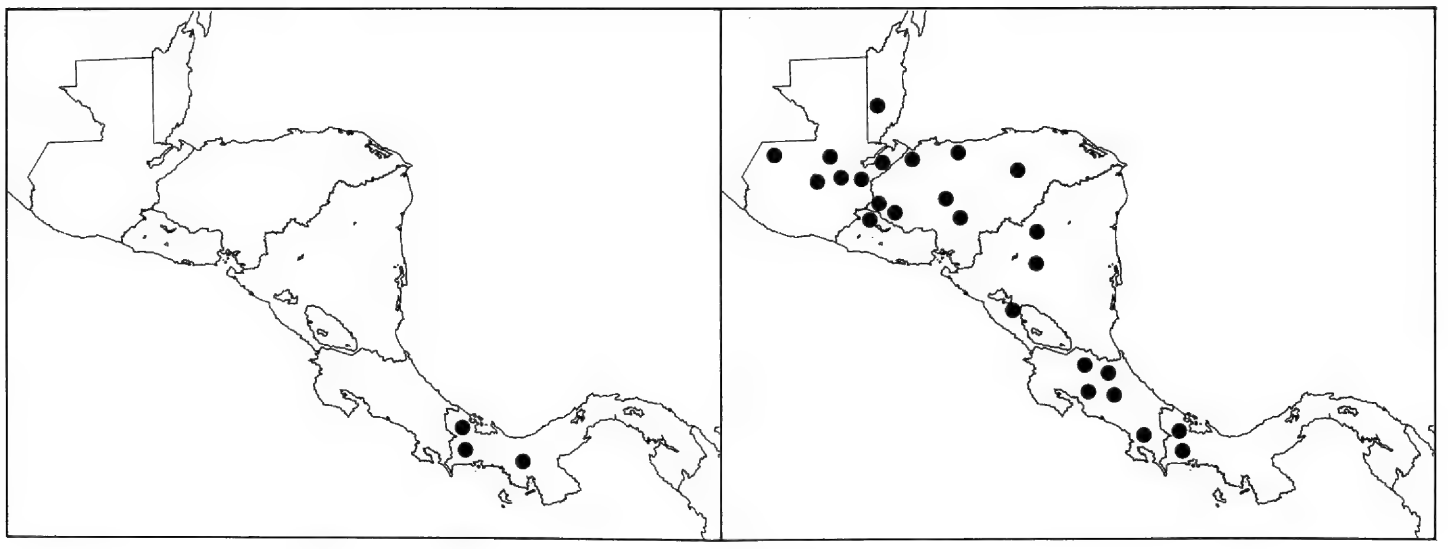


Figure 82. *Renauldia paradoxica*. A. Habit. B. Median leaf cells. C, E & G. Leaves. D. Leaf apex. F. Pseudoparaphyllia. H. Basal and alar cells. Scale in mm: bar = 0.06 (B, D, H); bar = 0.08 (F); bar = 0.9 (C, E, G); bar = 5.1 (A). B, D, F, H from *Crosby 10154*; all other figure parts from *Allen 5265*.



Renauldia paradoxica *Phyllogonium fulgens*

Secondary stems irregularly spaced, erect, stipitate, irregularly pinnate-branched, 3–8 cm long; stems in cross section with sclerodermis of 2–4 rows of small, reddish yellow, thick-walled cells, cortical cells enlarged, yellowish to hyaline, firm- to thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous. Primary stem leaves erect to imbricate, ovate, abruptly narrowed to long flexuose apices, to 1.0 mm long, not decurrent; ecostate. Secondary stem and branch leaves closely spaced, erect-spreading when dry, 2.5–4.2 mm long, ovate to obovate, deeply concave, rarely somewhat rugose, with long, narrow flexuose acumina, auriculate and clasping at base, not decurrent; margins entire below, weakly serrulate above; costa none; cells linear-flexuose, thick-walled and porose throughout, smooth, 35–85 × 6–10 μm, cells of the acumen and auriculate base somewhat shorter; alar cells orange red, weakly developed, in a small, bulging-excavate group, somewhat enlarged, rhombic to short-rectangular cells across the leaf base orange red, thick-walled. Dioicous (?). Perigonia, perichaetia, and sporophytes unknown.

Illustrations. Allen (1987g, Figs. 1–8). Figure 82.

Habitat. Pendent from canopy branches or on ground in very wet places; 350–1700 m.

Distribution in Central America. PANAMA. Bocas del Toro: *Allen 5265* (MO); Chiriquí: *Allen 5509B* (MO); Veraguas: *Crosby 10220* (FH, MO).

World range: Central America; Western and Northern South America.

Renauldia paradoxica is a pendent, canopy moss very similar in aspect to *Schliephackea*. The species sometimes grows on the ground in very wet places. The secondary nature of this terrestrial habitat, however, is demonstrated by the co-presence in the collections of *Macromitrium*. Under proper conditions, many epiphytic genera (*e.g.*, *Orthostichella*) are able to maintain themselves after falling to the ground. *Schliephackea* is in the Dicranaceae; it differs from *R. paradoxica* in having a strong single costa, sharply serrate leaf margins, and well-developed alar cells.

The evenly foliate stems and strongly concave, long narrowly acuminate leaves of *R. paradoxica* are distinctive features of the species. Furthermore, its ecostate leaves that are auriculate at base, porose leaf cells, and sharply differentiated, excavate alar cells separate *R. paradoxica* from all other members of the Pterobryaceae in Central America.

The name "*paradoxica*" was given to this species because of uncertainty about its generic position. There is evidence in its features to support a placement in *Renauldia*, *Hildebrantiella*, *Orthostichidium*, and *Pterobryopsis*. *Hildebrantiella* differs from it most clearly in having numerous inflated alar cells and strongly decurrent leaves. Most species in *Orthostichidium* have strongly ranked leaves, but in some species the leaves are unranked. *Pterobryopsis* typically differs from *R. paradoxica* in having singly costate leaves; however, there are ecostate species of *Pterobryopsis*. All four genera are in need of revision, and until then this species seems best placed in *Renauldia*.

Renauldia paradoxica differs from all species of *Renauldia* in having long, narrowly acuminate leaves and sharply differentiated, excavate alar cells. Within *Renauldia* it appears closest to the African *R. dusenii* (Broth.) Broth., which also has a pendent habit and auriculate leaves.

Excluded taxa

Spiridentopsis longissima (Raddi) Broth., Nat. Pflanzenfam. I(3): 806. 1906.

This monospecific genus was reported from Central America on the basis of a single Panamanian collection (see Crosby 1969b) made by Berthold Seemann, and named by Wilson (1854) as "*Hypnum cirrifolium* Schwaegr. var. ?". The Seeman collection (in BM) is *Pilotrichella flexilis*.

PHYLLOGONIACEAE

Phyllogoniaceae Kindb., Bot. Centralbl. 76: 85. 1898.

By Ronald A. Pursell

Plants medium-sized to robust, golden brown to olive green, lustrous, usually in festoons. Primary stems prostrate, adhering tightly to substrate, with small, fragile, scale-like leaves; rhizoids smooth, castaneous, in clusters basal to leaves. Secondary stems densely foliate, irregularly branched, pendent; stems in cross section with small incrassate cells enclosing larger thin-walled cells, central strand absent; paraphyllia none; pseudoparaphyllia foliose; axillary hairs with 1–3 quadrate, pigmented basal cells and 2–5 elongate, hyaline distal cells; rhizoids similar to those of primary stems. Secondary stem and branch leaves erect-spreading, little altered when dry, distichous, equitant, conduplicate, more or less auriculate, cucullate; margins more or less entire, incurved distally; costae weakly short and double or absent; cells smooth, more or less incrassate, linear-flexuose, porose, shorter proximally and distally; alar cells differentiated, in small dark patches. Leaves of flagelliform branches erect-spreading, sometimes appressed, concave, not conduplicate, lanceolate, acute to acuminate. Dioicous. Perichaetia and perigonia axillary, inconspicuous or conspicuous. Setae short, smooth. Capsules stegocarpous, immersed or shortly exserted, erect, radially symmetric, exothecial cells quadrate to elongate, walls evenly thickened; stomata phaneroporous in proximal parts or absent; peristome diplolepideous, inserted just below capsule mouth; exostome teeth pale, smooth to finely papillose, prostome present or absent; endostome reduced or none. Spores finely papillose to verrucose. Calyptrae cucullate or mitrate, naked or pilose.

This monogeneric family (Lin 1983; Buck & Goffinet 2000; Goffinet & Buck 2004) is widespread in the Neotropics but is also found in southern Africa, the Subantarctic Islands, and the western Indian Ocean. Typically, the plants grow in complex festoons on branches and twigs of trees and shrubs, but on occasion they are terrestrial. The plants are best recognized by their distichous, equitant, conduplicate leaves of the secondary stems and branches. Laminal cells are linear-flexuose, smooth, and have moderately incrassate, porose walls. All species are dioicous. According to Lin (1983), the family is closely related to genera in the subfamily Pterobryoideae of the Pterobryaceae. Other genera in Central America with pendent plants are: *Barbella*, *Calyptothecium*, *Isodrepanium*, *Meteoridium*, *Meteorium*, *Neckera*, *Orthostichopsis*, *Pilotrichella*, *Squamidium*, and *Zelometeorium*. These genera should not be confused with *Phyllogonium*, because they lack distichous, equitant, conduplicate leaves. Three genera, however, with distichous, equitant, and conduplicate leaves are *Fissidens*, *Orthorrhynchium*, and *Sorapilla*. *Fissidens* is widespread in Central America, (Pursell 2007), but it is a haplolepideous, acrocarpous moss that never grows in festoons. *Orthorrhynchium* has leaves similar in appearance to those of *Phyllogonium*, and although once considered to belong to the Phyllogoniaceae, it has been allotted its own family (Lin 1983), based on laminal cell differences, a lack of pseudoparaphyllia, and the presence of well-developed preperistomes, smooth exostomes, and lack of endostomes. Moreover, the genus is known only from New Caledonia, Australia, and New Zealand. *Sorapilla*, a pleurocarpous genus, with leaves closely resembling those of *Fissidens*, has been shown by Allen (1981) to have diplolepideous peristomes, of which the exostomes are greatly reduced. Although *Sorapilla* is epiphytic, it does not form complex festoons, and the single Neotropical species is known only from Ecuador. *Bryoxiphium*, an acrocarpous moss with distichous leaves that have dorsal extensions from the costae and an eperistomate sporophyte, is terrestrial or saxicolous, and is not known from Central America.

1. *Phyllogonium* Brid., Bryol. Univ. 2: 671. 1827.

Plants medium-sized to robust, lustrous, golden brown to olive green, sometimes dark brown to black, especially in older parts, usually in complex festoons on limbs and branches, occasionally terrestrial. Primary stems dark castaneous, prostrate, attached tightly to substrate, irregularly branched, with small, fragile, scale-like leaves; stems in cross section with small incrassate cells enclosing larger thin-walled cells, central strand absent; rhizoids smooth, castaneous, in clusters basal to dorsal

sides of leaves. Secondary stems and branches densely foliate, irregularly branched, pendent; paraphyllia none; pseudoparaphyllia foliose; axillary hairs with 1–3 more or less quadrate, pigmented basal cells and 2–5 elongate, hyaline distal cells, distalmost cells obtuse to rounded; rhizoids similar to those of primary stems. Secondary stem and branch leaves altered little when dry, erect-spreading, smooth or undulate, distichous, equitant, conduplicate, oblong, more or less auriculate, cucullate, truncate to retuse-pungent and erect to strongly pungent and recurved but not retuse; margins more or less entire, incurved distally; costae weakly short and double or absent; cells unistratose, smooth, linear-flexuose, shorter distally and proximally, more or less incrassate, porose; alar cells differentiated, in small, dark patches; leaves of flagelliform branches erect-spreading, sometimes more or less appressed, concave, not conduplicate, pungent to acuminate. Asexual propagula none. Dioicous. Perichaetia and perigonia gemmiform, axillary, inconspicuous or conspicuous; perichaetial leaves more or less convolute, oblong-ovate, concave, not conduplicate, abruptly acuminate; perigonial leaves oblong-ovate, concave, acuminate. Setae short, smooth, dark castaneous; vaginulae more or less pilose. Capsules shortly exserted or immersed, erect, radially symmetric, cylindric to urceolate, castaneous or pale yellow; exothecial cells irregularly quadrate to irregularly oblong, incrassate, walls evenly thickened; stomata phaneroporous in proximal parts or absent; opercula conic, obliquely long-rostrate; annuli of 1–3 tiers of incrassate, oblate cells. Peristome diplolepideous, double or single, inserted just below capsule mouth, prostome sometimes present, exostome inflexed when dry, erect when moist, teeth pale, margins irregular, smooth to finely papillose, ventral trabeculae well developed; endostome (lacking in *P. viride*) greatly reduced, basal membranes low, segments rudimentary. Spores more or less spherical, finely papillose to verrucose. Calyptrae cucullate or mitrate, naked or more or less pilose.

Phyllogonium has three species, all of which are found in Central America. The genus is distinguished by its golden brown to olive green plants that typically form festoons on the branches of trees and shrubs, but on occasion can be terrestrial. Secondary stems and branches are densely foliate, with distichous, equitant, conduplicate, and cucullate leaves. The leaves are more or less auriculate, with differentiated alar regions, and linear-repand, porose median laminal cells. Differences in their leaf apices are the best means of distinguishing the species. In *P. fulgens* and *P. viride*, the apices are pungent, the former retuse-erect and the latter strongly recurved but not retuse. In *P. viscosum*, the leaf apices are truncate. Unfortunately, the leaf apices in all three species are somewhat variable. For example, in *P. fulgens* the pungent apices can be somewhat curved, in *P. viride* some apices can be retuse, and in *P. viscosum* some apices can be somewhat pungent. According to Buck (1998), the primary stems turn about 90° to give rise to pendent secondary stems; the primary stems then continue forward growth by buds that form near the base of secondary stems. Fecundity is very low in the genus as a result of the dioicous condition of the plants. Asexual propagation, although not demonstrated, is probably by fragmentation of leaves and leafy branches.

The name *Phyllogonium* combines the Greek *phyllo* (leaf) with *gonia* (angled or angular); according to Bridel (1827), the name refers to the inclusion of the female gametangia within the doubled or conduplicate leaves.

1. Leaves undulate when dry, strongly auriculate; leaf apices truncate, sometimes retuse-pungent, straight; capsules exserted . . . . . 3. *P. viscosum*
1. Leaves smooth, more or less auriculate; leaf apex pungent or retuse-pungent; capsules exserted or immersed 2

2. Leaf apices retuse-pungent, straight to slightly recurved; capsules exserted . . . . . 1. *P. fulgens*
2. Leaf apices pungent, strongly recurved, not retuse; capsules immersed . . . . . 2. *P. viride*

1. *Phyllogonium fulgens* (Hedw.) Brid., Bryol. Univ. 2: 671. 1827. *Pterigynandrum fulgens* Hedw., Sp. Musc. Frond. 86. 1801. *Pterogonium fulgens* (Hedw.) Sw., Fl. Ind. Occid. 3: 1776. 1806. Protologue. In arboribus rupibusque Jamaicae, *Swartz.* Type (see Lin 1983). In arboribus rupibusque Jamaicae, *s. coll.* (G, holotype).

Phyllogonium aureum Mitt., J. Linn. Soc., Bot. 12: 424. 1869. *Phyllogonium fulgens* var. *aureum* (Mitt.) Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 41(1): 81. 1905. Protologue. Ins. Jamaica, *March, Maxwell,*

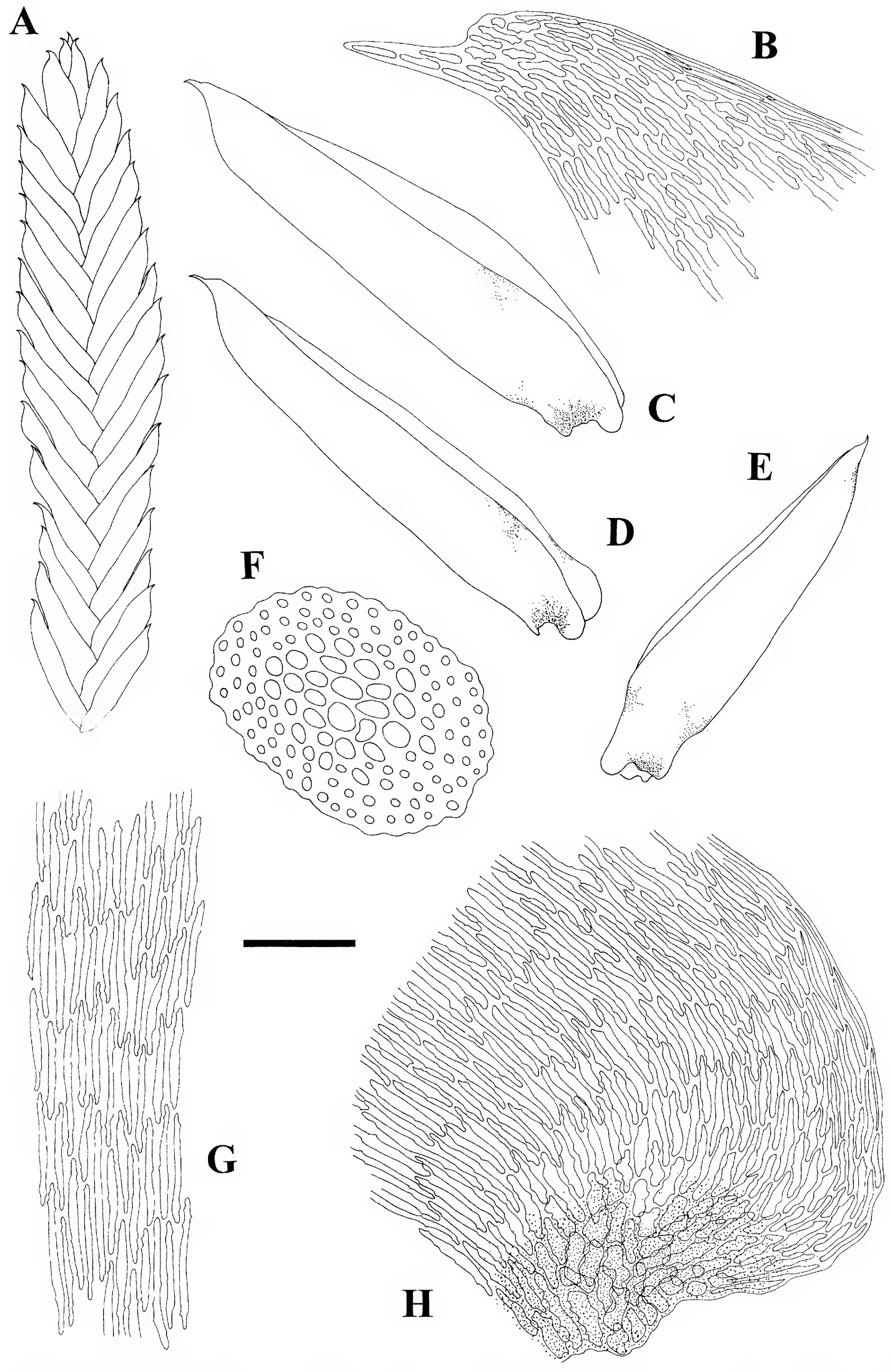


Figure 83. *Phyllogonium fulgens*. A. Habit. B. Leaf apex. C–E. Leaves. F. Stem in cross section. G. Median leaf cells. H. Basal and alar cells. Scale in mm: bar = 0.05 (F); bar = 0.06 (B, G, H); bar = 0.5 (C–E); bar = 1.56 (A). All figure parts from *Allen 17358*.

Wilds, Wilson; S. Christophori [Saint Kitts], *Breutel*. Andes Peruvianae, in monte Guayrapurina ex arborum ramis pendulum (3000 ped.), *Spruce, 1178*. Type (see Florschütz 1964). *March 461*, Jamaica (NY, lectotype). Lin (1983) superfluously selected *Spruce 1178* as lectotype.

Phyllogonium globitheca Müll. Hal., Bull. Herb. Boissier 5: 563. 1897. Protologue. Jamaica, Morces Pass, 4900 ped. altum, ad truncos, 24 Aprili 1896: *W. Harris*. Hb. Jamaicense *N° 10,049*. Types (see Lin 1983). Morces Gap. 4900 ped altum, ad truncos, 24 April, 1896, *Harris 10049* (H, lectotype; BM, NY, isolectotypes).

Phyllogonium goebelii Müll. Hal., Flora 83: 338. 1897. Protologue. Venezuela, Cumbre de Caracas, [*Goebel*] *37*. Type (see Lin 1983). Venezuela, Cumbre de Caracas, *Goebel s.n.* (H, lectotype).

Phyllogonium fulgens (Hedw.) Brid. var. *gracile* Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 41(1): 80. 1905. Protologue. Costarica: collines de Santiago, (*Aman Breues*; herb W. Mönkemeyer). Type. Costarica: collines de Santiago. Leg. *Aman Breues*, 1901 (NY, isotype).

Phyllogonium fulgens (Hedw.) Brid. var. *rufescens* S. H. Lin, J. Taiwan Mus. 36: 60. 1983. Protologue. [Colombia] Tequendama in sylv. ad arbor. pendal, alt. 2600 m, Jan. 1860, *Lindig 2087*. Types (see Lin 1983). Colombia: Tequendama in sylv. ad arbor. pendal, alt. 2600 m, Jan. 1860, *Lindig 2087* (BM, holotype; BM, H, NY, isotypes), *syn. nov.*

Plants typically robust, lustrous, golden brown to olive green, sometimes dark brown to black, especially in older parts, in complex festoons. Primary stems dark castaneous, irregularly branched, prostrate, attached tightly to substrate; stems in cross section with 2–5 layers of small, incrassate cells enclosing larger, thin-walled cells, walls of all cells pigmented, outer cells usually darker, inner cells often resorbed, central strand absent; rhizoids smooth, castaneous, in clusters basal to dorsal side of fragile, acute to acuminate scale-like leaves more or less appressed to stems. Secondary stems and branches densely foliate, irregularly branched, pendent, to 50 cm long, often becoming more or less flagelliform distally; paraphyllia absent; pseudoparaphyllia obtusely foliose; axillary hairs with 1–2 short, pigmented basal cells and 2–3 elongate, hyaline distal cells; rhizoids similar to those of primary stems; leaves more or less unchanged when dry, erect-spreading, usually loosely imbricate, distichous, equitant, conduplicate, oblong-lanceolate, usually weakly auriculate, cucullate, mostly retuse-pungent, apices erect, sometimes somewhat recurved, at times truncate-dentate, 2.0–3.7 × 1.2–2.0 mm, fragile when dry, often only basal parts present on older secondary stems and branches; margins more or less entire, incurved distally; costae short, double, and indistinct or absent; cells linear-repand, smooth, more or less incrassate, porose, median cells 41–81 × 3–6 μm, apical cells shorter, auricular cells shorter; alar cells differentiated in small clusters, dark castaneous, rounded-quadrate to oblong; leaves of distal flagelliform branches erect-spreading to sometimes appressed, more or less concave, not conduplicate, lanceolate. Asexual propagula none. Dioicous. Perigonia and perichaetia gemmiform, axillary; perigonial and perichaetial leaves ovate to ovate-oblong, acute to acuminate, concave; apical cells more or less obtuse to rounded. Setae 1.8–1.9 mm long, smooth, castaneous. Capsules castaneous, shortly exserted, erect, radially symmetric, ovate to cylindric, 1.4–1.8 mm long; exothecial cells irregularly quadrate to irregularly oblong, incrassate, walls more or less evenly thickened; stomata on lower parts of capsules; opercula conic, obliquely long-rostrate, 1 mm long; peristome diplolepideous, inserted just below capsule mouths, incurved when dry, erect when wet, prostomes rudimentary or none; exostome teeth narrowly triangular, often joined distally, margins uneven, pale, smooth or finely papillose, median line faint, dorsal trabeculae weak, ventral trabeculae low; endostomes rudimentary. Spores 18–23 μm, verrucose. Calyptrae cucullate, castaneous, sparingly pilose (also naked, Lin 1983), hairs 3–5-seriate proximally, uniseriate distally, cells incrassate, distal cells longer than proximal cells.

Illustrations. Bartram (1949, Fig. 123 A–B); Florschütz (1964, Fig. 105); Lin (1983, Pl. 1, Pl. 2 a–b, Fig. 3); Sharp *et al.* (1994, Fig. 550); Churchill (1994, Fig. 31 B); Churchill and Linares (1995, Fig. 142 a–g); Duarte Bello (1997, Pl. 208); Buck (1998, Pl. 62 8–13); Gradstein *et al.* (2001, Fig. 162); Buck (2003, Fig. 116). Figure 83.

Habitat. Usually in complex festoons on tree or shrub trunks, branches, and twigs in forests (especially cloud forests), along trails, overhanging streams, and in pastures, infrequently on rotted logs and soil of road cuts; 350–2400 m.

Distribution in Central America. BELIZE. Cayo: *Whittemore 6254* (MO). GUATEMALA. Alta Verapaz: *Sharp 3004* (MO); Baja Verapaz: *Sharp 5198* (F); El Progreso: *Sharp 2729* (MO, NY, US);

Huehuetenango: *Steyermark 48807* (F, FH); Izabal: *Steyermark 41935* (F, FH); Zacapa: *Steyermark 42866* (F, FH, NY, US). EL SALVADOR. Chalatenango: *Winkler 44* (MO). HONDURAS. Atlántida: *Allen 17358* (MO); Comayagua: *Allen 11037* (MO); Cortés: *Allen 14188* (MO); Francisco Morazán: *Standley 13403* (F); Lempira: *Allen 12001* (MO); Ocotepeque: *Allen 14432* (MO); Olancho: *Allen 12848* (MO). NICARAGUA. Granada: *Stevens 4386* (MO); Jinotega: *Stevens 11752* (MO); Matagalpa: *Davidse et al. 30506* (MO). COSTA RICA. Alajuela: *Standley & Torres 47515* (FH, NY, US); Cartago: *Crosby 6337* (MO); Heredia: *Crosby 6474* (MO); Puntarenas: *Lyon 522* (MO); San José: *Standley 38723* (FH, NY, US). PANAMA. Bocas del Toro: *Allen 5315* (MO); Chiriquí: *Allen 5421* (MO).

World range: Mexico; Central America; Caribbean; Western and Northern South America, Brazil.

Phyllogonium fulgens and *P. viride* are much alike. Both species have smooth leaves that are little changed when dry, and the auricles of both are less developed than those in *P. viscosum*. Flagelliform branches with mostly erect-spreading, concave but not conduplicate leaves are common in *P. fulgens*. In *P. viride* the distal branch leaves, although smaller than those on older branches, are conduplicate. Gametophytically, these two species can be distinguished by differences in their leaf apices: *P. fulgens* mostly retuse-pungent and erect; *P. viride* pungent, strongly recurved, and not retuse.

Phyllogonium fulgens has been divided into three varieties: var. *fulgens*, var. *gracile* Renauld & Cardot, and var. *rufescens* Lin. Variety *fulgens* is considered to have only conduplicate leaves, while the variety *gracile* has flagelliform branches with lanceolate to narrowly lanceolate, non-conduplicate leaves. Many collections from Central America, particularly those from Costa Rica and Panama, conform to variety *gracile*. However, in some collections, *e.g.*, *Lyon 522* (MO) from Costa Rica, a clear transition from conduplicate to lanceolate leaves occurs. Moreover, there are collections, *e.g.*, *Allen 12001* (MO) from Honduras and *Allen 5260A* (MO) from Panama, in which there are only a few flagelliform branches. The differences between these two varieties seem to be a matter of degree, which might be due to the differences in the age of the plants or variations in microenvironmental conditions. Lin (1983) described var. *rufescens* from a single Colombian collection that differed from the typical variety in having red brown plants with narrower branches, more closely arranged, shorter leaves in which the sinuses are shallow, and the leaf apices short. An examination of an isotype (NY) reveals that the characters on which this variety is based are only minor variations from the typical variety.

Phyllogonium fulgens is the most widespread species of the genus in Central America, occurring in all seven countries. Sporophytes were found in only 1.7% (3 out of 172) of the Central American collections examined. Lin (1983) erroneously listed W as the place of deposition of the holotype of *P. fulgens*; Florschütz (1964) clearly indicated that the type is located in G.

2. *Phyllogonium viride* Brid., Bryol. Univ. 2: 673. 1827. *Phyllogonium fulgens* (Hedw.) Brid. var. *viride* (Brid.) Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32(1): 184. 1893. *Phyllogonium viscosum* (P. Beauv.) Mitt. var. *viride* (Besch.) Paris, Index Bryol. Suppl. 269. 1900. Protologue. In Brasiliae arboribus pendulum habitat, comm. Persoon. Type (see Lin 1983). In brasiliae arboribus pendulum habitat, *s. coll.* (B, holotype).

Plants typically robust, lustrous, golden brown to olive green, older parts sometimes dark brown to black, in complex festoons. Primary stems dark castaneous, irregularly branched, prostrate, attached tightly to substrate; stems in cross section with 4–6 rows of small, incrassate, pigmented cells, cortex of larger, thin-walled, hyaline (sometimes pigmented) cells, central strand absent; rhizoids smooth, castaneous, in clusters basal to dorsal side of fragile, appressed, acute to acuminate scale-like leaves. Secondary stems and branches densely foliate, irregularly branched, in complex festoons, to 30 cm long; paraphyllia none; pseudoparaphyllia foliose, obtuse; axillary hairs with 1–2 short, pigmented basal cells and 2–5 elongate, hyaline distal cells, the terminal cells more or less obtuse. Secondary stem and branch leaves erect-spreading, more or less unchanged when dry, distichous, equitant, conduplicate, more or less auriculate, cucullate, not retuse, pungent, strongly recurved, oblong-lanceolate, 1.4–4.0 × 1.2–1.8 mm; margins more or less entire, incurved distally; costae short, double, at times indistinct or ecostate; cells linear-repand, smooth, incrassate, porose, median cells 29–68 μm long, distal and auricular cells shorter; alar cells differentiated, in small clusters, dark castaneous, rounded-quadrate to oblong. Asexual propagula none. Dioicous. Perigonia and perichaetia gemmiform, axil-

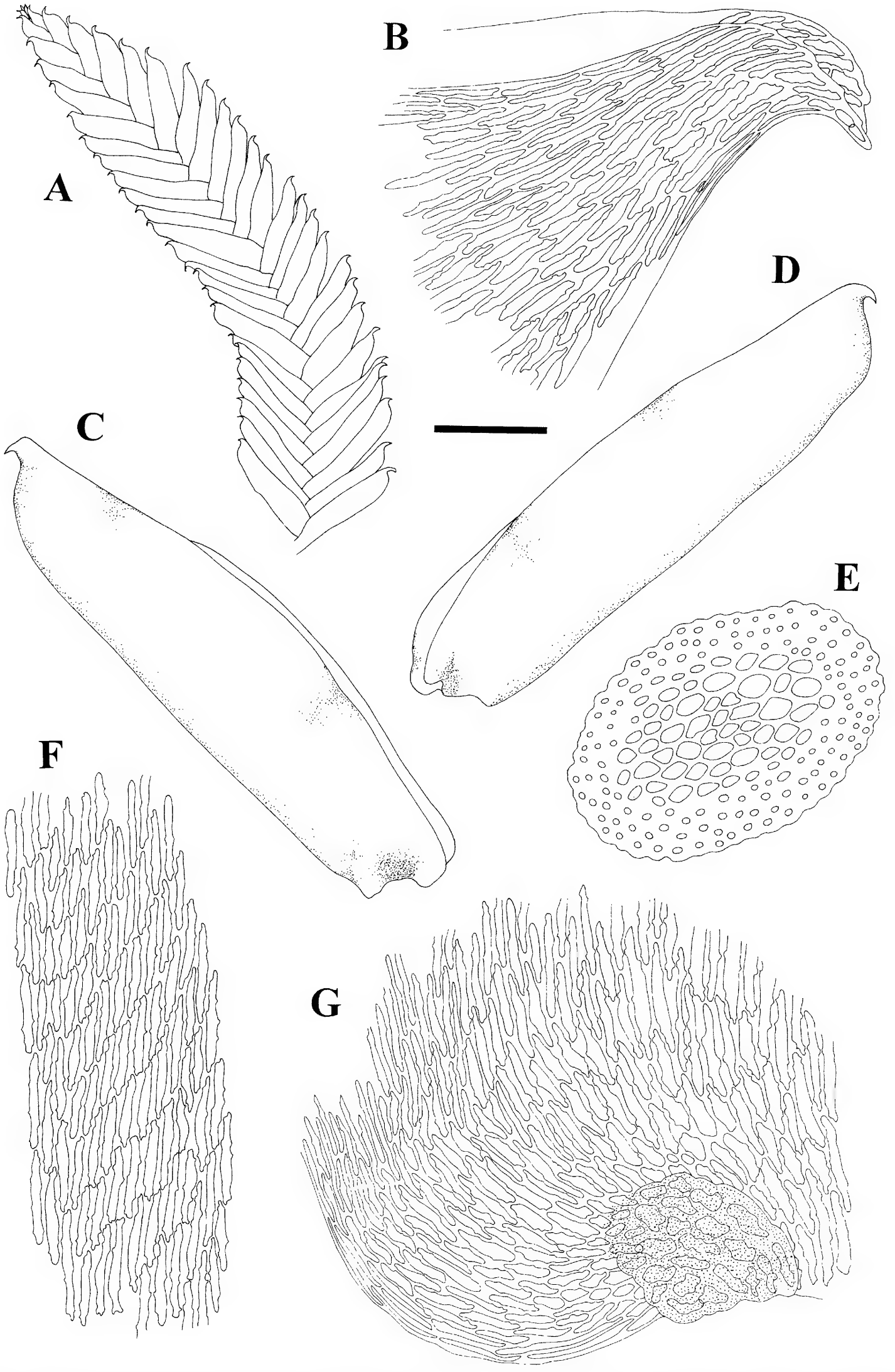
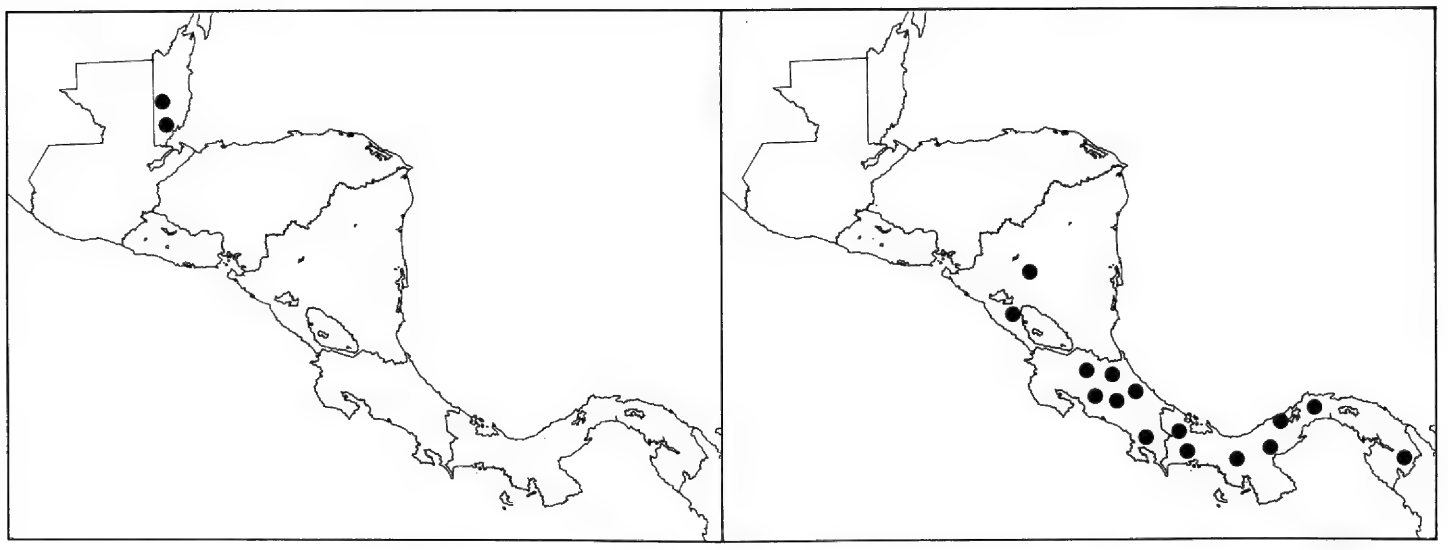


Figure 84. *Phyllogonium viride*. A. Habit. B. Leaf apex. C & D. Leaves. E. Stem in cross section. F. Median leaf cells. G. Basal and alar cells. Scale in mm: bar = 0.06 (B, E–G); bar = 0.5 (C, D); bar = 2.6 (A). All figure parts from *Allen 18822*.



Phyllogonium viride *Phyllogonium viscosum*

lary. Sporophytes not seen in Central American collections, description from Brazilian specimens. Setae short, 0.2–0.5 mm long, smooth, castaneous or yellow. Capsules immersed, erect, radially symmetric, ovate to cylindric, castaneous or yellow, 2.2–2.5 mm long; exothecial cells irregularly quadrate to irregularly oblong, thin- to medium-walled; stomata absent; opercula conic, short- to long-rostrate, 0.6–0.8 mm long; peristome diplolepideous, single, prostome present, fragmentary; exostome teeth inserted just below capsule mouth, incurved when dry, erect when wet, pale, linear-triangular, more or less denticulate, median line and dorsal trabeculae faint, ventral trabeculae low; endostome absent. Spores anisosporous, 18–29 μm and 32–56 μm, smooth to faintly papillose. Calyptrae not seen, description from Lin (1983), small, 0.8–1.2 × 0.29–0.48 mm, cucullate or mitrate, entire at base, extending to the base of opercula, densely hairy, hairs filamentous, articulate, flexuose, smooth.

Illustrations. Brotherus (1906c, Fig. 619 G, as *Phyllogonium immersum*); Brotherus (1925, Fig. 563 G, as *Phyllogonium immersum*); Lin (1983, Pl. 4, Fig. 5); Buck (1998, Pl. 61 1–7); Yano (1996, Figs. 43–56). Figure 84.

Habitat. In forests, mostly on branches and trunks of living trees, sometimes on rotted tree trunks; 685–1000 m.

Distribution in Central America. BELIZE. Cayo: *Allen 15045* (MO); Toledo: *Allen 18829* (MO).

World range: Mexico; Central America; Caribbean; Western and Northern South America, Brazil; Subantarctic Islands; Western Indian Ocean.

In Central America *Phyllogonium viride* occurs only in Belize. Neither gametangia nor sporophytes were found on the eight Central American collections available for study. Sporophytes from South American collections of *P. viride* have immersed capsules, unlike those of *P. fulgens* and *P. viscosum*, which are exserted. Gametophytically, the species closely resembles *P. fulgens*, but the leafy stems and branches are somewhat broader. Lin (1983) indicated that the dry leaves of *P. viride* are longitudinally striate, but this condition can also be seen in some specimens of *P. fulgens*. In the absence of sporophytes, the presence of strongly recurved, pungent, non-retuse apices on most leaves of *P. viride* is the best feature separating it from *P. fulgens*. The leaves of *P. viride*, however, are variable; sometimes those at the branch tips can be truncate, or the pungent apices of some leaves can be straight. The leaves on ultimate branches, although smaller than those of older branches, are always conduplicate and never concave.

Lin (1983) reported *Phyllogonium viride* from Costa Rica and Honduras. The Costa Rican specimen (*Brenes 20589*, NY), however, is *Phyllogonium fulgens*. The Honduran collection (*Schipp S-868*, NY) from "British Honduras" is actually from Belize.

3. *Phyllogonium viscosum* (P. Beauv.) Mitt., J. Linn. Soc., Bot. 12: 423. 1869. *Pterigynandrum viscosum* P. Beauv., Prodr. Aethéogam. 87. 1805. *Pterigynandrum fulgens* Hedw. var. *viscosum*

(P. Beauv.) Brid., Muscol. Recent. Suppl. 1: 137. 1806. *Pterogonium viscosum* (P. Beauv.) Schwägr., Sp. Musc. Suppl. 1 (1): 109. 1811. *Phyllogonium fulgens* (Hedw.) Brid. var. *viscosum* (P. Beauv.) Brid., Bryol. Univ. 2: 673. 1827. Protologue. Cette espèce a été rapportée par M. M. Dupetit-Thouars et Bory-St-Vincent, des Iles de France [Mauritius] et de Bourbon [Réunion]. Le premier en a trouvé une variété dans l'Ile de Tristan d'Acunha [Tristan da Cunha], *Bory s.n.* Types (see Lin 1983). Ins. Bourbon, *Bory s.n.* (JE, lectotype; NY, isotype); Tristan d'Acunha, *Dupetit-Thouars s. n.* (BM, syntype).

Phyllogonium speciosum Müll. Hal., J. Mus. Godeffroy 3(6): 70. 1874. Protologue. Costa Rica, Naranjo: *A. S. Oersted*, Quito [Ecuador]: *H. Karsten*, Nova Granada [Colombia]: Triana. Type (see Lin 1983). *Oersted s.n., p.p.* (H, lectotype).

Phyllogonium serra Müll. Hal., J. Mus. Godeffroy 3(6): 70. 1874. Protologue. Nova Granada [Colombia], Fusagasugà, ad arborum pedes, *A. Lindig* 1861 legit. Type (see Lin 1983). Nova Granada, Fusagasugà, ad arborum pedes, *Lindig s.n.* (BM, lectotype).

Plants typically robust, lustrous, golden brown to olive green, older parts sometimes dark brown to black, in complex festoons. Primary stems dark castaneous, irregularly branched, prostrate, attached tightly to substrate; stems in cross section with 2–6 rows of small, incrassate, pigmented cells, cortical cells larger, pigmented, thin-walled, often resorbed, central strand absent; rhizoids smooth, castaneous, in clusters basal to dorsal side of scale-like, fragile, acute to acuminate leaves more or less appressed to stem. Secondary stems and branches densely foliate, irregularly branched, pendent, to 40 cm or more long; paraphyllia none; pseudoparaphyllia foliose, obtuse; axillary hairs with 2–3 short, pigmented basal cells and 3–4 elongate, hyaline distal cells; rhizoids similar to those of primary stems, infrequent; leaves loosely imbricate, usually irregularly undulate when dry, distichous, equitant, conduplicate, oblong-ovate, strongly auriculate, cucullate, truncate to sometimes retuse-pungent, 3.5–4.7 × 1.2–1.7 mm, fragile when dry, often only basal parts present on older stems and branches; costae short, double, indistinct or ecostate; cells unistratose, smooth, somewhat incrassate, porose, median cells 43–83 × 5–11 μm, distal and auricular cells shorter; alar cells differentiated, in small clusters, dark castaneous, rounded-quadrate to oblong. Asexual propagula none. Dioicous. Perigonia and perichaetia gemmiform, axillary. Setae 2.5–4.0 mm long, smooth, castaneous. Capsule shortly exserted, erect, radially symmetric, ovate to cylindric, castaneous, 2.3–2.8 mm long; exothecial cells irregularly quadrate to irregularly oblong, walls more or less evenly thickened; stomata restricted to proximal parts; opercula conic, obliquely long-rostrate, 0.5 mm; peristome diplolepideous and double, inserted just below mouths of thecae, prostomes fragmentary; exostome teeth narrowly triangular, often joined at the tips, margins uneven, pale, smooth or finely papillose, median line and dorsal trabeculae faint, ventral trabeculae low; endostomes rudimentary. Spores 18–31 μm, smooth to finely papillose. Calyptrae not seen, description from Lin (1983), mitrate-cylindrical, 2.0–2.3 × 0.32–0.40 mm, scabrate distally, entire at base, sparingly hairy; hairs filamentous, sometimes 2–5-stratose, serrate proximally, thick-walled, sometimes longer than calyptrae, caducous.

Illustrations. Brotherus (1906c, Fig. 619 A–F, as *Phyllogonium serra*); Brotherus (1925, Fig. 563 A–F, as *Phyllogonium serra*); Lin (1983, Pl. 3, Fig. 4); Sharp *et al.* (1994, Fig. 551 a–g); Churchill and Linares (1995, Fig. 143 h–j); Buck (1998, Pl. 62 1–7). Figure 85.

Habitat. In forests (especially cloud forests) and pastures, commonly pendent in complex festoons on tree trunks and branches, less often on twigs and branches of shrubs, rotting logs, buttress roots, ferns (e.g., *Asplenium auriculatum*), and soil of road cuts and slopes; 16–2400 m.

Distribution in Central America. NICARAGUA. Granada: *Baker 2529* (F, FH, MO, NY, US); Matagalpa: *Richards et al. 3795* (F, FH, MO, NY). COSTA RICA. Alajuela: *Brenes 19070* (F, FH); Cartago: *Hammel 18323* (CR, MO); Heredia: *Crosby 6578* (MO); Limón: *Gómez 18501* (CR, MO); Puntarenas: *Lyon 115* (MO); San José: *Standley 38857* (FH, NY, US). PANAMA. Bocas del Toro: *Allen 5687* (MO); Chiriquí: *Maxon 5700* (F, FH, NY, US); Coclé: *Dwyer et al. 45038* (MO); Colón: *Crosby 10381* (MO); Darién: *Allen 8882* (MO); Panamá: *Crosby 4360* (F, MO, NY, US); Veraguas: *Nee 11335* (MO).

World range: Mexico; Central America; Caribbean (*Reyes Montoya 1018*, NY); Northern and Western South America; Western Indian Ocean (La Réunion), Southern Africa.

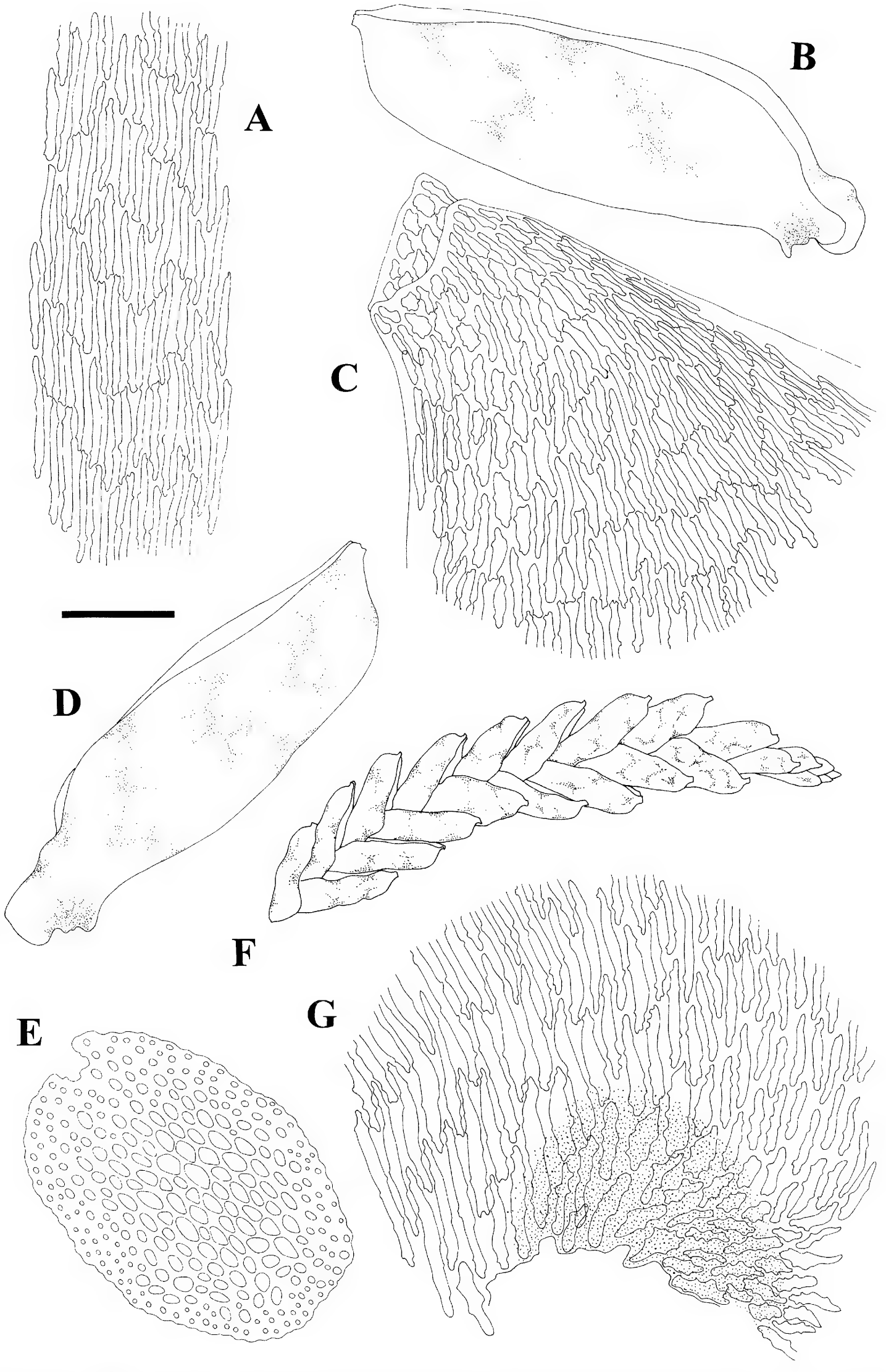


Figure 85. *Phyllogonium viscosum*. A. Median leaf cells. B & D. Leaves. C. Leaf apex. E. Stem in cross section. F. Habit. G. Basal and alar cells. Scale in mm: bar = 0.06 (A, C, G); bar = 0.08 (E); bar = 0.9 (B, D); bar = 3.2 (F). All figure parts from *Lyon 122*.

Phyllogonium viscosum is the easiest *Phyllogonium* species to recognize because of its turgid habit. When dry the leaves are tumid and irregularly undulate, thus masking its distichous and conduplicate features. Moreover, the leaf auricles are developed to a greater degree in *P. viscosum* than in either *P. fulgens* or *P. viride*. The leaf apices in *P. viscosum* are primarily truncate, unlike the strongly pungent apices of *P. fulgens* and *P. viride*. Nevertheless, some leaves of *P. viscosum* can be slightly pungent. *Pilotrichella flexilis* can sometimes be confused with *P. viscosum*, because the species are similar in color, grow in pendent masses, and have auriculate leaves with recurved mucros and linear-repand, porose laminal cells. However, the leaves of *Pilotrichella flexilis* are concave rather than conduplicate and consistently ecostate.

Sporophytes of *Phyllogonium viscosum*, like those of *P. fulgens*, are exserted on short setae. Among the three species of *Phyllogonium*, fecundity is greatest in *P. viscosum*; sporophytes were found in 13 of the 157 Central American specimens studied (8.3%).

CATAGONIACEAE

Catagoniaceae W. R. Buck & Ireland, Nova Hedwigia 41: 115. 1985.

Stems and branches terete to complanate-foliate, prostrate or erect-ascending, simple or irregularly branched; stems in cross section with epidermis of 1 row of small, thick-walled cells, cortical cells enlarged, central strand absent; paraphyllia absent; pseudoparaphyllia absent; rhizoids from small clusters of initials abaxial to the leaf insertions, papillose-roughened, not or sparsely and irregularly branched. Stem and branch leaves similar, pseudodistichous, concave to asymmetrically conduplicate, rounded to shortly auriculate or straight at base, not decurrent; margins serrulate above, entire below or entire throughout; costae short and double, or absent; cells linear-flexuose, smooth, non-porose; alar cells undifferentiated. Asexual reproduction occasionally by uniseriate, rhizoidal gemmae. Dioicous. Setae elongate, smooth. Capsules erect or inclined; exothecial cells not or somewhat collenchymatous; stomata phaneroporic, long-pored; opercula conic to conic-rostrate; annulus present; peristome diplolepideous, exostome narrowly triangular, median line faint, densely cross-striate and papillose on lower dorsal surface, papillose above; endostome papillose, basal membranes high, segments narrow, keeled, perforate, cilia 1–3. Calyptrae cucullate.

The Catagoniaceae are a small, monogeneric family. The family is nearly restricted to the Southern Hemisphere, where it occurs in southern South America, southern Africa, the Mascarene Islands, New Guinea, Australasia, and the Subantarctic Islands. One species (*C. brevicaudatum*) extends into the Northern Hemisphere: Colombia, Venezuela, Central America, and Mexico. The family has stems with an outer layer of sclerodermal cells, no pseudoparaphyllia, and mostly unbranched, papillose rhizoids that originate from clusters of initials abaxial to the leaf insertions. Its leaves are pseudodistichous, concave to asymmetrically conduplicate, and lack alar cell development. The family has hypnaceous peristomes and cucullate calyptrae. The Catagoniaceae were established by Buck and Ireland (1985) for a group of species previously placed in the Phyllogoniaceae or Plagiotheciaceae. They differ from the Phyllogoniaceae in lacking creeping stolons and pseudoparaphyllia, but having papillose rhizoids, pseudodistichous, strongly concave to asymmetrically concave leaves, and hypnaceous peristomes. The Plagiotheciaceae, as narrowly circumscribed by Buck and Ireland (1985), differ in having leaves with well-developed alar cells that extend into long decurrencies and stems with a distinctive hyalodermis. Pedersen and Hedenäs (2001, 2002) greatly expanded the Plagiotheciaceae to include a large number of disparate and clearly unrelated genera. Their studies, however, often aligned *Catagonium* with *Herzogiella*, *Isopterygiopsis*, or *Pseudotaxiphyllum*, all genera of the Hypnaceae. Buck and Ireland (1985) separated the Catagoniaceae from the Hypnaceae because of its conduplicate leaves, but the leaves of *Isopterygiopsis* are just as strongly conduplicate as those of *Catagonium*.

1. *Catagonium* Müll. Hal. *ex* Broth., Nat. Pflanzenfam. I(3): 1087. 1908.

Hypnum Hedw. sect. *Catagonium* Müll. Hal., Flora 68: 425. 1885, invalid name, lacks a description.
Catagonium Müll. Hal. *ex* Broth. sect. *Eucatagonium* Broth., Nat. Pflanzenfam. I(3): 1088. 1908, illegitimate name.
Eucatagonium M. Fleisch. *ex* Broth., Nat. Pflanzenfam. (ed. 2) 11: 177. 1925, illegitimate name, includes a genus with priority.

Plants small to medium-sized, glossy, golden to yellowish green, in dense (occasionally loose) mats, at times pendent. Stems and branches terete to complanate-foliate, prostrate or erect-ascending, simple or irregularly branched, at times long-attenuate or flagelliform; stems in cross section with epidermis of 1 row of small, thick-walled cells, cortical cells enlarged, central strand absent; paraphyllia and pseudoparaphyllia absent; rhizoids from small clusters of initials abaxial to the leaf insertions, papillose-roughened, reddish brown, not or sparsely and irregularly branched. Stem and branch leaves similar, closely or somewhat distantly spaced, pseudodistichous, lanceolate-ovate to ovate-oblong, concave to asymmetrically conduplicate, abruptly acuminate to piliferous, rounded to shortly auriculate or straight at base, not decurrent; margins serrulate above, entire below or entire

throughout, incurved on one side at base and sometimes above; costae short and double, or absent; cells linear-flexuose, smooth, non-porose, shorter near the apex; alar cells undifferentiated. Asexual reproduction occasionally by uniseriate, rhizoidal gemmae. Dioicous. Setae elongate, smooth. Capsules erect or inclined, oblong to cylindric, exothecial cells not or somewhat collenchymatous; stomata phaneroporic, long-pored; opercula conic to conic-rostrate; annuli present; peristome diplolepideous; exostome narrowly triangular, median line faint, densely cross-striate and papillose on lower dorsal surface, papillose above; endostome papillose, basal membranes high, segments narrow, keeled, perforate, cilia 1–3. Calyptrae cucullate, smooth, naked.

The genus *Catagonium* was revised by Lin (1984). He recognized four species, only one of which is found in Central America. The genus is distinguished by its glossy, yellowish green plants that typically form dense, terrestrial mats. Occasionally, the genus occurs on rocks or tree trunks; rarely, it can be pendent. The stems and branches lack paraphyllia and pseudoparaphyllia, and are densely or loosely foliate, with strongly concave to asymmetrically conduplicate leaves. The rhizoids in *Catagonium* are densely papillose and originate from small clusters of initials positioned abaxial to the leaf insertion; they are unbranched or sparsely, irregularly branched. The leaves are strongly incurved to shortly auriculate at base, lack alar cell differentiation, and have very short, double costae and linear-flexuose leaf cells. Although reported to lack asexual reproduction (Lin 1984), *Catagonium* occasionally has rhizoidal gemmae. The sporophytes of *Catagonium* have a distinct annulus, long-pored stomata, and a hypnaceous peristome.

Lin (1984) considered *Catagonium* close to *Isopterygiopsis* because of the presence in both of: (1) distinctly complanate, conduplicate leaves; (2) truncate-shaped leaf insertion; (3) non-decurrent leaves; (4) short, double or absent costae; (5) entire leaf margins; (6) lack of pseudoparaphyllia; (7) dioicous sexual condition; and (8) differentiated annuli. Both species also have papillose rhizoids. *Isopterygiopsis* differs from *Catagonium* in having rhizoids that originate from the leaf axils and a distinct stem hyalodermis. The genus has also been associated with *Phyllogonium*, *Isopterygium*, and *Plagiothecium*. *Phyllogonium* differs from *Catagonium* in having strongly creeping stolons; smooth rhizoids; foliose pseudoparaphyllia; distichous, symmetrically conduplicate leaves with porose leaf cells; and smooth to finely papillose exostomes with reduced or absent endostomes. *Isopterygium* differs from *Catagonium* in having filamentous pseudoparaphyllia. *Plagiothecium* differs from *C. brevicaudatum* in having leaves with well-developed alar cells that extend into long decurrencies and stems with a distinctive hyalodermis.

The name *Catagonium* combines the Greek prefix *cata* (downwards or outwards) with *gonia* (angled or angular), perhaps in reference to its conduplicate leaves.

Catagonium brevicaudatum Müll. Hal. *ex* Broth., Nat. Pflanzenfam. I(3): 1088. 1908. *Catagonium brevicaudatum* Müll. Hal., Nuovo Giorn. Bot. Ital. n. ser. 4: 150. 1897, invalid name, genus invalid at time of publication. *Isopterygium brevicaudatum* (Müll. Hal.) Paris, Index Bryol. Suppl. 218. 1900, invalid combination. *Eucatagonium brevicaudatum* (Müll. Hal. *ex* Broth.) Broth., Nat. Pflanzenfam. (ed. 2) 11: 178. 1925, invalid name, genus illegitimate. Protologue. Bolivia, Unduavi, 12,000 ped. altum inter *Polytrichadelphum vigens*: Dr. med *H. H. Rusby* Oct. 1885 sterile legit.

Plants small to medium-sized, lustrous, golden to yellowish green, in dense (occasionally loose) mats, at times pendent. Stems and branches complanate-foliate, 2–10 cm long, prostrate or erect-ascending, irregularly branched, at times long-attenuate, yellowish green when young, becoming red with age; stems in cross section with epidermis of 1–2 rows of small, thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia and pseudoparaphyllia absent; rhizoids from small clusters of initials abaxial to the leaf insertions, papillose-roughened, reddish brown, not or sparsely and irregularly branched; axillary hairs 3–6 cells long, basal 2–3 cells short-rectangular, reddish brown, upper 1–3 cells elongate, hyaline. Stem and branch leaves similar, 0.8–1.8 mm long, closely or somewhat distantly spaced, pseudodistichous, ovate to ovate-oblong, concave to asymmetrically conduplicate, abruptly ending in piliferous, recurved acumina, rounded to shortly auriculate at base; margins entire, incurved on one side at base and sometimes above; costae short and double, or absent; cells smooth, firm-walled, upper cells vermicular, 15–40 × 3–6 μm, median cells linear-flexuose, 60–100 × 2.5–4.0 μm; basal cells linear-oblong; alar cells undifferentiated. Asexual reproduction

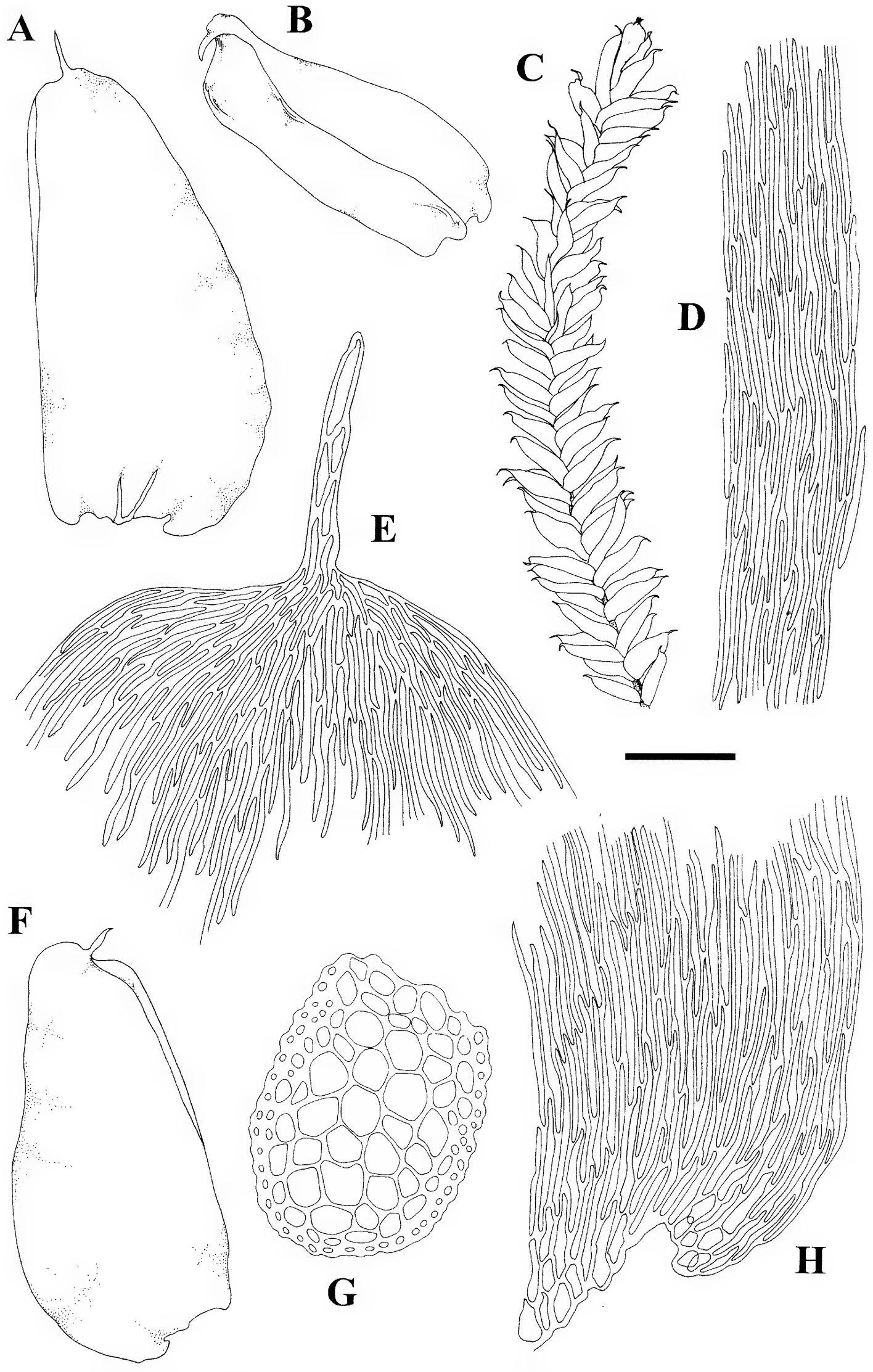
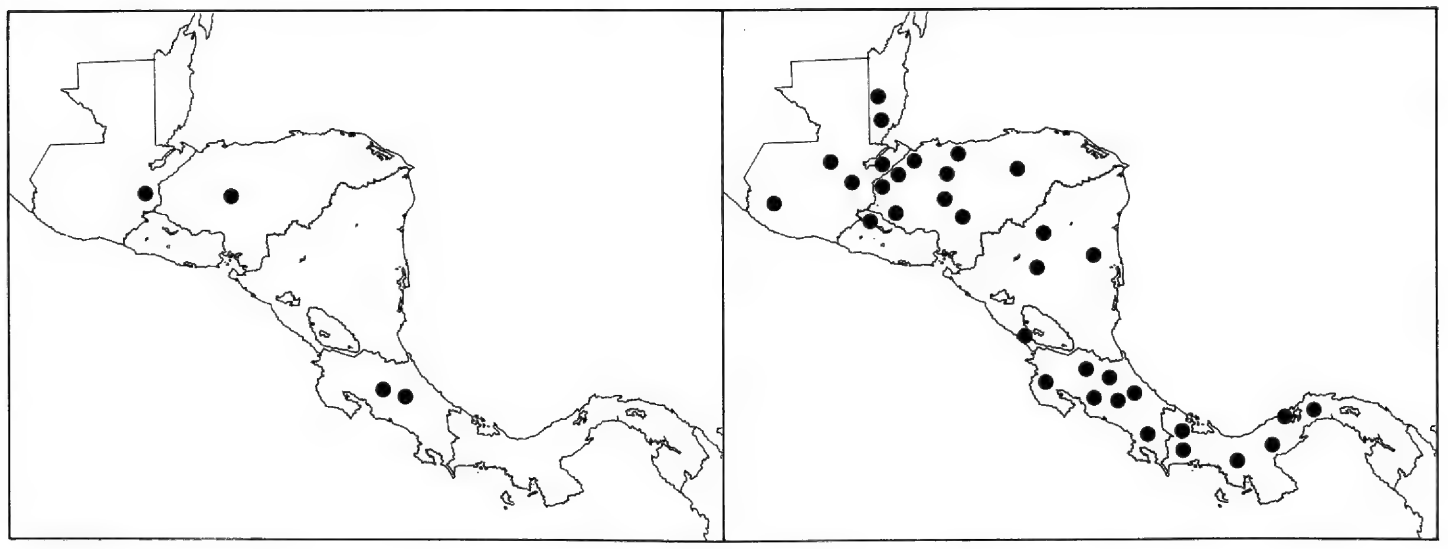


Figure 86. *Catagonium brevicaudatum*. A, B & F. Leaves. C. Habit. D. Median leaf cells. E. Leaf apex. G. Stem in cross section. H. Basal and alar cells. Scale in mm: bar = 0.05 (D, E, H); bar = 0.06 (G); bar = 0.28 (A, B, F); bar = 1.56 (C). All figure parts from *Holz 00-0643*.



Catagonium brevicaudatum *Homalia glabella*

occasionally by uniseriate, rhizoidal gemmae. Dioicous. Sporophytes not known in Central America. Only one, immature and badly damaged sporophyte from Colombia (*Cleef & Jaramillo-M 237*, MO) seen, description from Lin (1984). Setae elongate, 9.5 mm long. Capsules inclined, oblong, apophyses absent, 1.6–1.7 mm long; exothecial cells quadrate to rectangular, medium-walled; stomata on neck; peristome double, hypnoid, prostome absent, exostome papillose, median line thin, dorsal trabeculae thin, dorsal lamellae striate-papillose, ventral surface smooth; endostome not described. Spores rounded, 10–12 μm, densely papillose. Calyptra not described.

Illustrations. Bartram (1949, Fig. 123 C–E, as *Eucatagonium politum*); Lin (1984, Pl. 9); Buck and Ireland (1985, Fig. 9 A–E); Sharp *et al.* (1994, Fig. 725); Churchill and Linares (1995, Fig. 51 a–d); Gradstein *et al.* (2001, Fig. 103 G–J). Figure 86.

Habitat. On ground, logs, and vertical rock faces, at times in cloud forests; 1700–3260 m.

Distribution in Central America. GUATEMALA. Chiquimula: *Steyermark 31017* (F, FH). HONDURAS. Comayagua: *Allen 12304* (MO). COSTA RICA. Cartago: *Crosby & Crosby 6138* (MO); San José: *Standley & Valerio 43764a* (FH, NY, US).

World range: Mexico; Central America; Western and Northern South America, Brazil.

In Central America, *Catagonium brevicaudatum* is known from only a few high elevation localities. It typically grows terrestrially in dense mats, but also is found on rocks and occasionally pendent. The species has complanate-foliate stems that are typically irregularly branched, but there are numerous arrested branch primordia along the stems. If these primordia all gave rise to branches, the stems would be irregularly pinnately branched. The leaves are ovate to ovate-oblong, concave to asymmetrically conduplicate, shortly auriculate at base, and characteristically end abruptly in short, piliferous, recurved acumina. The leaf margins are erect to plane above, with the basal margin on one side often broadly incurved, and they are entire. The costae are very short and double or absent. The leaf cells in *C. brevicaudatum* are long and narrow: vermicular near the apex and linear-flexuose below. They are smooth throughout, and the alar cells are undifferentiated. The sporophytes of *C. brevicaudatum* are exceedingly rare, and the incomplete sporophyte description in Lin (1984) seems to indicate he did not see fully formed sporophytes. The only features observed on the single, damaged sporophyte examined are: (1) seta smooth, brownish red; (2) operculum conic-rostrate, 0.5 mm long; (3) capsule symmetric; (4) annulus present; (5) exothecial cells rounded to short-oblong, firm-walled, not collenchymatous; and (6) stomata phaneroporic and long-pored.

In Central America, *Catagonium brevicaudatum* could be mistaken for an *Isopterygium* or *Plagiothecium* because of its small size and complanate leaves that have linear-flexuose cells and short, double costae. *Isopterygium* is also similar to *C. brevicaudatum* in lacking alar cell differentiation, but all species of *Isopterygium* differ from *Catagonium* in having filamentous pseudoparaphyllia. All species of *Plagiothecium* differ from *C. brevicaudatum* in having leaves with well-developed alar cells that extend into long decurrencies and stems with a distinctive hyalodermis.

NECKERACEAE

Neckeraceae Schimp., Coroll. Bryol. Eur. 99. 1855 [1856].

Homaliaceae Schimp., Syn. Musc. Eur. CXLIV. 1860.
Neckeraceae Schimp. subfam. Thamnioideae Broth., Nat. Pflanzenfam. I(3): 851. 1906, illegitimate name.
Thamniaceae (Broth.) Mönk. in Rabenh., Deutschl. Krypt.-Fl. 3rd ed., 2(3) 647. 1927, illegitimate name.
Thamnobryaceae Margad. & During, Bekn. Fl. Ned. Blad-Leverm. 443. 1982. Thamnobryaceae W. R. Buck & Vitt, Taxon 35: 33. 1986, superfluous name.

Plants small, medium-sized, or robust, flattened, sometimes with an intense blackish color. Primary stems creeping, sympodially branched, often stoloniferous, occasionally pendent; rhizoids from circular clusters of initials abaxial to the stolon leaf insertions and at the base of secondary stems; leaves reduced, widely spaced, appressed to spreading. Stems horizontal or erect, not stipitate or stipitate-frondose, sometimes pendent, irregularly branched, complanate-foliate, at times flagellate-attenuate; cross section of secondary stems with sclerodermis, enlarged cortical cells, central strand present or absent; paraphyllia present or absent; pseudoparaphyllia present or absent. Stipe leaves erect, erect-spreading, or squarrose. Secondary stem and branch leaves symmetric or asymmetric, smooth or undulate, decurrent or rarely not decurrent; margins often inflexed on one side below, sometimes coarsely dentate at apex, occasionally with intramarginal limbidia; costae double or single, long or short, often forked or branched near tip, sometimes ending in a small spine on the dorsal surface; cells smooth or prorate; alar cells weakly differentiated. Asexual reproduction sometimes by deciduous leaves or filiform, microphyllous branchlets. Dioicous, synoicous, or autoicous. Perichaetia at times ramentose. Setae elongate or short, smooth throughout or smooth below and mammillose above. Capsules immersed or exserted, erect to suberect, symmetric or asymmetric; stomata present or absent; opercula rostrate; peristome diplolepideous; exostome teeth, linear or narrowly triangular, dorsal surface cross-striate below or papillose; endostome basal membranes low or high, segments perforate, keeled or not keeled, cilia well developed (nodose or appendiculate), rudimentary or absent. Calyptrae cucullate or mitrate and lobed, naked, sparsely hairy, densely ramentose, or smooth.

Goffinet and Buck (2004) listed 28 genera in the Neckeraceae, and with the addition of *Orthostichella* the family now consists of 29 genera. The Neckeraceae are most abundant and diverse in the tropics, especially in Southeast Asia. The family is poorly represented in the Northern Hemisphere, where it exhibits a small fraction of its remarkable variability and diversity. Traditionally, the Neckeraceae have been divided into two subfamilies: Neckeroideae and Thamnioideae. These subfamilies are sometimes treated at the family level (Buck & Vitt 1986; Sastre 1987; Churchill & Linares 1995; Gradstein *et al.* 2001). Enroth (1994b), however, demonstrated the impossibility of separating the two families because some genera in the group had the thamnioid gametophyte/neckeroid sporophyte combination of features, while others had the neckeroid gametophyte/thamnioid sporophyte combination. The use of a single family for this group of genera is now generally accepted (Enroth 1994b; He 1997; Buck & Goffinet 2000; Goffinet & Buck 2004).

Enroth (1994b) polarized the character states within the Neckeraceae, and, based on an analysis of their gametophytic and sporophytic characters, assigned relative advancement values for 23 genera. He concluded that some of the genera usually placed in the Thamnioideae were "clearly more primitive" than those placed in the Neckeroideae. Character state variability within the family is huge; however, a general gametophytic characterization of the Neckeraceae would include these features: (1) creeping stolons, with rhizoids more or less restricted to circular clusters just below the stolon leaf insertions; (2) stems often stipitate, with well-differentiated stipe leaves; (3) frondose branching pattern; (4) foliose pseudoparaphyllia; (5) the ability to form paraphyllia; and (6) leaves often complanate, with variously serrate margins, weakly developed alar cells, and firm, relatively short, upper leaf cells. Sporophytic characters within the Neckeraceae are so variable and oddly distributed in regards to gametophytic characters that it is impossible to present any generalized characterization of the Neckeraceae sporophyte. *Thamnobryum* appears to be the most primitive genus, while *Neckera* seems to be the most advanced genus of the Neckeraceae (see Enroth 1994b, Table 3).

Key to the genera in Central America

1. Branch leaves usually in spiral rows . . . . . 6. *Orthostichella*
1. Leaves never in spiral rows 2

2. Costae short and double 3
2. Costae long and single 5

3. Leaves oblong-lingulate, rounded at the apex, occasionally rounded-obtuse and apiculate . . . . . 1. *Homalia*
3. Leaves ovate-lanceolate or oblong-lanceolate or falcate-cultriform, apiculate, acute, or acuminate 4

4. Leaves falcate-cultriform, not or hardly undulate . . . . . 3. *Isodrepanium*
4. Leaves ovate-lanceolate or oblong-lanceolate, undulate . . . . . 4. *Neckera*

5. Branch leaves truncate; perichaetia sometimes with ramenta . . . . . 5. *Neckeropsis*
5. Branch leaves obtuse to acuminate; perichaetia without ramenta 6

6. Branch leaves rounded to the insertion, ± auriculate; leaves not or at times weakly complanate . . . . . 8. *Porotrichodendron*
6. Branch leaves not auriculate, at times weakly rounded to the insertions; leaves often complanate 7

7. Stipe without central strand . . . . . 2. *Homaliodendron*
7. Stipe with central strand (Central American taxa only) 8

8. Leaves with an intramarginal border of elongate cells; median leaf cells of branch leaves more or less isodiametric . . . . . 7. *Pinnatella*
8. Leaves without an intramarginal border of elongate cells; median leaf cells of branch leaves fusiform to linear 9

9. Costae of branch leaves strong, ending 7/8 the leaf length to subpercurrent, not or scarcely tapering at the apex . . . . . 10. *Thamnobryum*
9. Costae of branch leaves ending mostly 1/2–3/4 or more the leaf length, tapering to a slender point; OR costae on lower leaves tapering at the ends, 2/3 the leaf length, but upper leaves with percurrent costae filling the mucro . . . . . 9. *Porotrichum*

1. *Homalia* Brid., Bryol. Univ. 2: 812. 1827 ('*Omalia*'), name orthography conserved (Margadant & Geissler 1995). *Leskea* subg. *Omalia* Brid., Bryol. Univ. 2: 329. 1827. *Hypnum* sect. *Omalia* (Brid.) Müll. Hal., Syn. Musc. Frond. 2: 233. 1851. *Neckera* sect. *Omalia* (Brid.) Mitt., J. Proc. Linn. Soc., Bot. Suppl. 1: 117. 1859.

Plants small to large, strongly flattened, dark green to yellowish green, at times yellowish red, glossy. Primary stems creeping, often stoloniferous; rhizoids smooth, reddish brown, densely present on stolons and at the base of secondary stems; leaves appressed to spreading, oblong-ligulate. Secondary stems prostrate, not stipitate, irregularly branched, complanate-foliate, at times flagellate-attenuate; secondary stem cross section with sclerodermis, cortical cells enlarged, thick-walled, central strand absent or weakly developed; paraphyllia absent; pseudoparaphyllia present or absent. Secondary stem and branch leaves strongly flattened, wide-spreading, smooth when dry or wet, oblong, oblong-ligulate, or oblong-spathulate, 1.0–3.0 mm long, asymmetric, mucronate to rounded or truncate, apiculate or broadly acute, narrowly decurrent, straight at the insertion; margins inflexed on one side below, serrulate at apex, entire to subentire below; costae single and long, or faint, short, double or single; cells smooth, apical cells rounded, rhombic, or shortly fusiform, firm- to thick-walled, occasionally porose, median cells oblong-rhomboidal to linear-rhomboidal, thick-walled, basal juxtacostal cells linear-fusiform, thick- to firm-walled, porose; alar cells rectangular to oblong-rectangular, weakly differentiated, cells across the insertions porose. Asexual propagula absent. Dioicous. Perichaetial leaves ovate, sheathing at base. Setae elongate. Capsules erect to suberect, ovoid to oblong-ovoid, or oblong-cylindric, asymmetric; exothecial cells rounded, subquadrate to short-rectangular,

firm- or thick-walled; stomata on neck; opercula obliquely long-rostrate; annuli well developed; peristome diplolepideous; exostome teeth 16, narrowly triangular, dorsal surface densely cross-striate and papillose below, papillose above in vertical lines, trabeculae and median line well developed; endostome basal membranes high, segments subulate, broadly perforate, keeled, cilia well developed, 2–4, nodose or appendiculate. Calyptrae cucullate, smooth.

Homalia was revised by He (1997). The genus consists of five North Hemispheric species, only one of which (*H. glabella*) crosses into the Southern Hemisphere. Gametophytically, the genus is characterized by its glossy, strongly flattened stems that either lack or have a weakly developed central strand. Its stems are complanate-foliate, with oblong-ovate to oblong-spathulate, plane-margined leaves inserted in 8 ranks. All *Homalia* species have rounded, obtuse or broadly acute leaf apices and smooth cells that are rhombic to irregularly rhomboidal at the apex. The costae in *Homalia* vary considerably between species; some species have long, single costae, while in others they are short, faint, and can be either single or double on leaves from the same plant. The *Homalia* sporophytes have long setae, with erect to suberect capsules, well-developed annuli, and stomata. *Homalia* has a perfect, hypnaceous peristome, with broad exostome teeth that are densely cross-striate on the lower dorsal surface and an endostome with a high basal membrane, broadly perforate segments, and 2–4 well-developed cilia.

The systematic position of *Homalia* within the family is uncertain because it presents the classic moss dilemma: gametophytic features supporting one placement, but sporophytic features that support another. In this case, the gametophytes of *Homalia* closely resemble the genera associated with the subfamily Neckeroideae, while its sporophytes are identical to those found in the subfamily Thamnioideae. Fleischer (1908), Brotherus (1925), and Walther (1983) have aligned *Homalia* with the Neckeroideae; Sastre (1987) and Gradstein *et al.* (2001) place the genus in the Thamnobryaceae on the basis of its perfect hypnaceous peristome. However, because of the radically differing relationships implied by the different generations in *Homalia*, it is impossible to determine its generic relationships based solely on morphology.

The name *Homalia* is from the Greek *homalos* (even or level) and refers to the characteristically flattened stems and branches of this genus.

Homalia glabella (Hedw.) Schimp., Syn. Musc. Eur. 571. 1860. *Leskea glabella* Hedw., Spec. Musc. Frond. 235. 1801. *Neckera glabella* (Hedw.) F. Weber & D. Mohr, Index Mus. Pl. Crypt. 3. 1803. *Hypnum glabellum* (Hedw.) Sw. *ex* P. Beauv., Prodr. Aethéogam. 64. 1805. *Omalia glabella* (Hedw.) Schimp. *in* B.S.G., Bryol. Eur. 5: 54. 1850 (fasc. 44–45). Protologue. Jamaica, *Swartz.*

Hypnum defoliatum Müll. Hal. *in* Hampe, Bot. Zeitung (Berlin) 27: 457. 1869. *Homalia defoliata* (Müll. Hal.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 297. 1877. Protologue. Brasilia, Rio de Janeiro, *s. coll. & s.n.*

Plants medium-sized to large, 3–13 cm long, strongly flattened, dark green to yellowish green, at times yellowish red, glossy. Primary stems (stolons) creeping; rhizoids smooth, reddish brown, densely present on stolon and at the base of primary stems; leaves appressed to spreading, oblong-ligulate. Secondary stems prostrate, not stipitate, irregularly branched, complanate-foliate, at times flagellate-attenuate; secondary stems in cross section with sclerodermis of 3–6 rows of small, thick-walled cells, cortical cells enlarged, thin- to firm-walled, central strand weakly developed; paraphyllia absent; pseudoparaphyllia narrowly foliose to filamentous. Secondary stem and branch leaves strongly flattened, wide-spreading, smooth when dry or wet, oblong, oblong-ligulate, or oblong-spathulate, 1.0–3.0 mm long, asymmetric, mucronate to rounded or truncate, apiculate, at times broadly acute, narrowly decurrent, straight at the insertion; margins inflexed on one side below, serrulate at apex, entire to subentire below; costae usually faint, short, double or single, only rarely reaching 1/3 the leaf length; cells smooth, apical cells rounded, rhombic, or shortly fusiform, 15–35 μm long, firm- to thick-walled. occasionally porose, median cells oblong-rhomboidal to linear-rhomboidal, 45–85 μm long, thick-walled, basal juxtacostal cells linear-fusiform, thick- to firm-walled, porose; alar cells rectangular to oblong-rectangular, weakly differentiated, cells across the insertions porose. Asexual propagula absent. Dioicous. Perichaetial leaves ovate, sheathing at base. Setae elon-

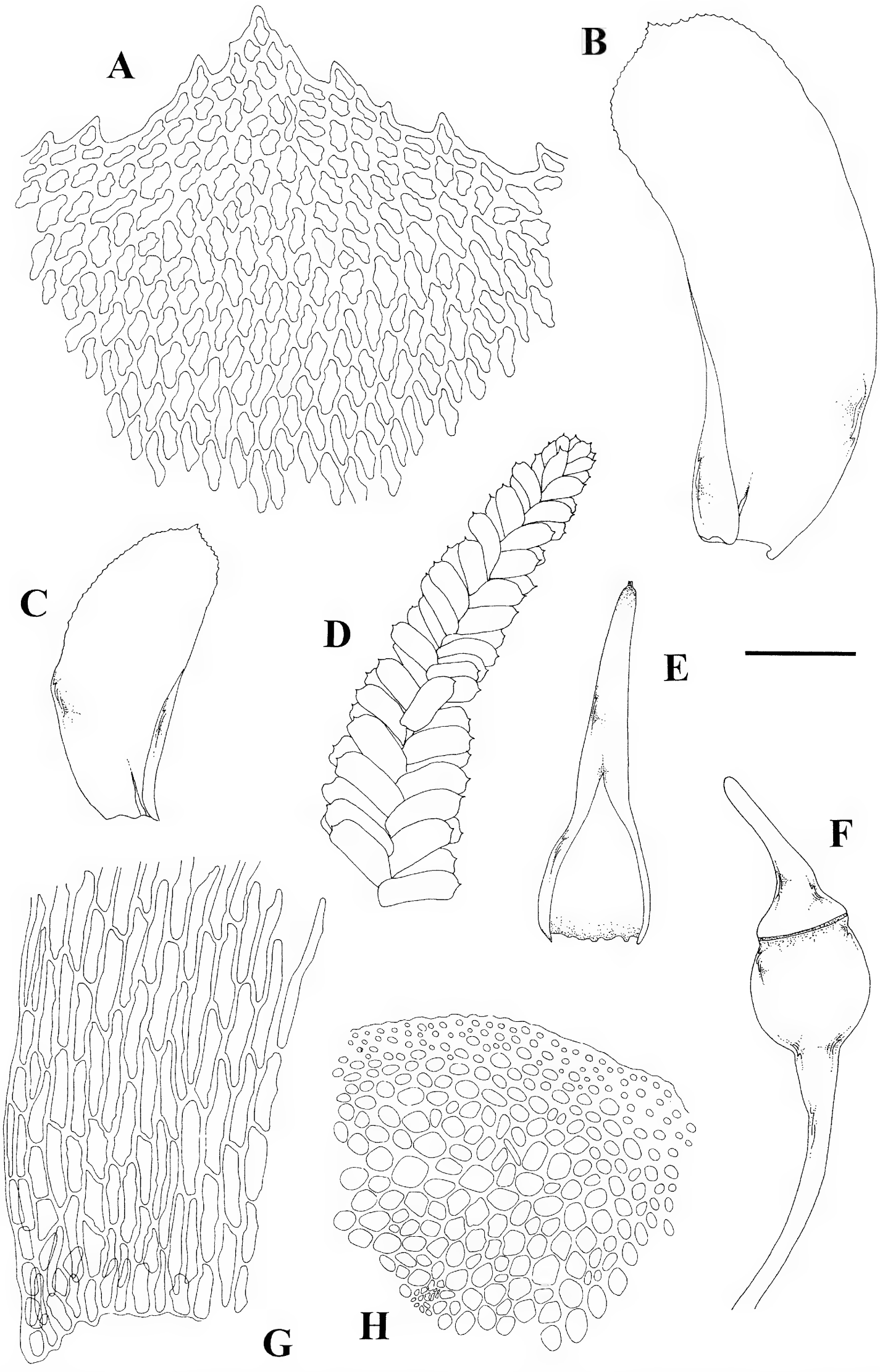


Figure 87. *Homalia glabella*. A. Leaf apex. B. Leaf. C. Leaf from *defoliata* form. D. Habit. E. Calyptra. F. Seta, capsule, and operculum. G. Basal and alar cells. H. Stem in cross section. Scale in mm: bar =0.06 (A, G); bar = 0.08 (H); bar = 0.7 (B, C); bar = 0.9 (E); bar = 1.0 (F); bar = 3.2 (D). C from *Allen 15193*; E, F from *Allen 11314*; all other figure parts from *Allen 18573*.

gate, 1–2 cm long, smooth, yellowish brown to red. Capsules suberect, ovoid to oblong-ovoid, asymmetric, 1.0–2.5 mm long; exothecial cells not strongly differentiated at mouth, those below rounded, subquadrate to short-rectangular, firm- or thick-walled; stomata on neck; opercula obliquely long-rostrate, 2.0–2.5 mm long; annuli well developed, of a layer of enlarged, thick-walled, fragmenting cells; peristome diplolepideous; exostome teeth yellow to yellowish brown, narrowly triangular, 0.6–0.7 mm long, dorsal surface densely cross-striate and papillose below, vertically papillose above, trabeculae and median line well developed; endostome yellow, lightly papillose throughout, basal membranes well developed, 0.2–0.3 mm long, segments subulate, 0.5–0.7 mm long, broadly perforate, keeled, cilia well developed, 2–4, nodose. Spores 10–15 μm, lightly papillose. Calyptrae cucullate, smooth, to 4 mm long.

Illustrations. Hedwig (1801, Pl. 59 1–5); Bartram (1949, Fig. 126 E–G); Sharp *et al.* (1994, Fig. 560); Duarte Bello (1997, Pl. 209); He (1997, Figs. 90–115); Buck (1998, Pl. 42 1–7); Gradstein *et al.* (2001, Fig. 215 L–P). Figure 87.

Habitat. On boulders, rocks (often near streams), tree trunks, roots, and on logs; 110–3000 m.

Distribution in Central America. BELIZE. Cayo: *Allen 18321* (BRH, MO); Toledo: *Allen 18573* (BRH, MO). GUATEMALA. Alta Verapaz: *Standley 91483* (F, FH, NY); Izabal: *Steyermark 39056* (F, FH, NY); Quetzaltenango: *Steyermark 33345* (F, FH); Zacapa: *Steyermark 29931* (F, FH). EL SALVADOR. Santa Ana: *Davidse 37327A* (MO). HONDURAS. Atlántida: *Allen 17579* (MO, TEFH); Comayagua: *Allen 13794* (MO, TEFH); Copán: *Allen 17741* (MO, TEFH); Cortés: *Allen 14193* (MO, TEFH); Francisco Morazán: *Allen 12394* (MO); Lempira: *Allen 11992* (MO); Olancho: *Allen 12504* (MO); Santa Bárbara: *Allen 11685* (MO); Yoro: *Allen 13652* (MO). NICARAGUA. Jinotega: *Crosby 2741* (MO); Matagalpa: *Granzow de la Cerda & Moreno GC-1524b* (DUKE, MO); Rivas: *Stevens 6548* (MO); Zelaya: *Atwood 3113* (MO). COSTA RICA. Alajuela: *Liesner 5074* (CR, MO); Cartago: *Standley 33832* (FH); Guanacaste: *Standley 44737* (FH, MO, NY, US); Heredia: *Crosby 9663* (MO); Limón: *Gómez et al. 20457* (MO); Puntarenas: *Lyon 294* (MO); San José: *Crosby & Crosby 6392* (MO). PANAMA. Bocas del Toro: *Allen 5867* (MO); Chiriquí: *Cornman 3111* (F, MO, US); Coclé: *Hammel 13644* (MO); Colón: *Crosby 10444* (MO, PMA); Panamá: *Crosby 10426* (MO); Veraguas: *Knapp 2530* (DUKE, F, FH, H, MO, NY, PMA, US).

World range: Mexico; Central America; Caribbean; Northern South America, Brazil.

Plants of *Homalia glabella* are glossy, lack stipitate stems, and are remarkably flattened to the substrate. The species is fairly common in wet, shaded habitats in Central America, where it grows on rocks and boulders along streams and on tree trunks. When collected on wet rocks, the species is especially robust and dark, almost blackish green, while plants from bark tend to be smaller and yellowish green. The stems and branches of *H. glabella* are morphologically plastic and sometimes become transformed to stolons that then give rise to new primary stems. Unlike most other species of *Homalia*, the stems of *H. glabella* have a weakly developed central strand. The leaves of *H. glabella* are asymmetric, complanate, broadly rounded and sharply serrate at the apex, and they have short, nearly obsolete costae. Its leaf cells are smooth and elongate-fusiform, except near the apex, where they become rounded, rhombic, or shortly fusiform, and are often porose. *Homalia glabella* has long-exserted capsules and large, perfect, hypnaceous peristomes: exostome narrowly triangular, densely cross-striate on the lower dorsal surface; endostome basal membranes high, segments broadly perforate, cilia 2–4.

There is a fairly distinct Central American form of *H. glabella* that has deciduous leaves. In some collections (*e.g.*, *Allen 15193*, MO) of this form many of the stems and branches are fully denuded, while in others the feature is weakly expressed. The form only occurs on trees, and the plants are consistently yellowish green in color and usually much smaller than is typical for *H. glabella*. Furthermore, the leaves in this form are more spathulate than those of typical *H. glabella*, which usually are oblong in shape. The form appears to be nomenclaturally centered on the Brazilian *H. defoliata*. He (1997) synonymized *H. defoliata* with *H. glabella*, although he did not examine its type.

In Central America *Homalia glabella* could superficially be confused with any of the other Neckeraceae with complanate leaves. All *Neckeropsis* species differ from *H. glabella* in having long single costae and immersed capsules. Central American species of *Isodrepanium* and *Neckera* are never

strongly flattened to the substrate, and they have acute or acuminate leaf apices. *Isodrepanium lentulum* also differs from *H. glabella* in often having falcate-cultriform leaves, while the Central American species of *Neckera* differ in having undulate leaves.

2. *Homaliodendron* M. Fleisch., Hedwigia 45: 74. 1906.

Plants medium-sized to robust, stipitate-frondose, flattened, forming pale green to yellowish green, lax tufts. Stolons creeping; rhizoids smooth, reddish brown, densely present on stolons and at the base of stipitate stems; leaves appressed, widely spaced, evenly foliate, and triangular-lanceolate. Secondary stems erect, stipitate, irregularly bi- or tripinnate, complanate-foliate, at times flagellate-attenuate; secondary stems in cross section with sclerodermis, enlarged, firm-walled, cortical cells, central strand absent; paraphyllia absent; pseudoparaphyllia narrowly foliose to filamentous. Stipe leaves erect-spreading from an appressed base, evenly foliate, triangular to oblong-triangular, broadly acuminate, entire to subentire below, serrate to toothed above; margins plane; costae single or absent. Stem and branch leaves flattened, spreading to wide-spreading, smooth when dry or wet or somewhat plicate when dry, smooth when wet, broadly oblong-ovate, oblong-ligulate, obovate, or oblong-spathulate, asymmetric, narrowly decurrent, straight at the insertion; margins broadly inflexed on one side below, entire, serrate or coarsely dentate at apex, entire to subentire below; costae often spurred below, slender or strong, reaching 1/2–2/3 the leaf length; cells smooth or papillose, apical cells rounded-rhomboid to hexagonal, or shortly fusiform, firm- to thick-walled, occasionally porose, median cells oblong-rhomboidal, linear-rhomboidal, or long-rectangular, thick-walled, porose, basal juxtacostal cells linear-fusiform, thick- to firm-walled, porose, basal marginal cells rectangular to subquadrate; alar cells rectangular to oblong-rectangular, weakly differentiated, cells across the insertions porose. Asexual reproduction sometimes by microphyllous branches. Dioicous. Perigonia gemmiform, lateral on stems and branches. Perichaetia lateral on stems and branches, inner leaves ovate-sheathing at base, long-lanceolate and spreading above, entire, crenulate, serrate or dentate at apex. Setae elongate, smooth throughout or smooth below and mammillose above. Capsules ovoid-cylindrical; exothecial cells rectangular to subquadrate, thick-walled near mouth, short-rectangular, thick-walled below; stomata on neck; opercula conic, obliquely short-rostrate; annuli weakly differentiated; peristome diplolepideous; exostome teeth linear-lanceolate, papillose throughout or cross-striate at base on dorsal (outer) surface and papillose above; endostome basal membranes short, segments perforate and keeled, cilia absent or rudimentary. Spores papillose. Calyptrae cucullate, naked or sparsely hairy, smooth.

Homaliodendron is a genus of 23 species found in the tropical regions of the world. The genus, however, is concentrated in southeastern Asia; only four species are found in the Neotropics (*H. flabellatum*, *H. piniforme*, and *H. punctulatum* M. Fleisch.) and Africa (*H. flabellatum*, *H. piniforme*, and *H. exiguum* (Bosch & Sande Lac.) M. Fleisch.). The genus has stipitate stems that lack central strands. Its stipe leaves are erect at base and have plane margins. The secondary stems and branches are complanate-foliate, with oblong-ovate, oblong-ligulate, obovate, or oblong-spathulate, asymmetric leaves. The leaves have margins broadly inflexed on one side, long, single costae, and short, smooth, usually rhombic to irregularly rhomboidal upper leaf cells. The sporophytes of *Homaliodendron* have short setae, erect capsules, stomata, and poorly developed annuli. It has a reduced neckeraceous peristome with narrow exostome teeth that are mostly papillose, but can be cross-striate at the very base on the lower dorsal surface, and the endostome has a low basal membrane, narrow segments, and no cilia.

Enroth (1989) considered *Homaliodendron* closely related to *Homalia*. That genus differs from *Homaliodendron* in sometimes having a central strand in its stipe, long setae, and a perfect hypnaceous peristome: broad exostome teeth that are densely cross-striate on the lower dorsal surface; endostome with a high basal membrane, broadly perforate segments and 2–4 well-developed cilia. In Central America *Homaliodendron* can be confused with *Porotrichum* or *Thamnobryum*, because those genera have some species with strongly stipitate plants, as well as leaves with similar margins, areolation, and costal form. Intergradation between these genera and *Homaliodendron* is such that the only consistent difference between them is the presence of a central strand in the stipes and stems of

Porotrichum and *Thamnobryum*. The Indochinese species of *Homaliodendron* were revised by Ninh (1984).

The name *Homaliodendron* combines the generic name *Homalia* with the Greek *dendron* (tree).

1. Leaves coarsely dentate, dentations multicellular . . . . . 1. *H. flabellatum*
1. Leaves serrulate, serrations unicellular . . . . . 2. *H. piniforme*

1. *Homaliodendron flabellatum* (Sm.) M. Fleisch., Hedwigia 45: 74. 1906. *Hookeria flabellata* Sm., Trans. Linn. Soc. 9: 280. 1808. *Leskea flabellata* (Sm.) Schwägr., Sp. Musc. Frond. Suppl. 1(2): 164. 1816. *Hypnum flabellatum* (Sm.) Dicks. *ex* Müll. Hal., Syn. Musc. Frond. 2: 225. 1850. *Neckera flabellata* (Sm.) Mitt., J. Proc. Linn. Soc., Bot. Suppl. 1: 118. 1859, not *Neckera flabellata* Hampe, Linnaea 31: 525. 1862, illegitimate homonym. *Homalia flabellata* (Sm.) Bosch & Sande Lac., Bryol. Jav. 2: 58. 1863. *Porotrichum flabellatum* (Sm.) Mitt., Trans. Linn. Soc. London, Bot. 3: 175. 1891. *Thamnium flabellatum* (Sm.) Kindb., Hedwigia 41: 228. 1902, not *Thamnium flabellatum* Nog., Trans. Nat. Hist. Soc. Formosa 26: 39. 1936, illegitimate homonym. Protologue. [Caribbean] In Indiâ occidentali. Communicated to the younger Linnaeus by Mr. Dickson, as a native of the West Indies under the name of *Hypnum flabellatum*.

Pterygophyllum decompositum Brid., Bryol. Univ. 2: 764. 1827. *Neckera decomposita* (Brid.) Müll. Hal., Syn. Musc. Frond. 2: 42. 1850. *Leskea decomposita* (Brid.) Brid. *ex* Müll. Hal., Syn. Musc. Frond. 2: 42. 1850, invalid combination, listed in synonymy. *Porotrichum decompositum* (Brid.) Mitt., J. Linn. Soc., Bot. 12: 463. 1869. *Thamnium decompositum* (Brid.) Kindb., Hedwigia 41: 221. 1902. *Porothamnium decompositum* (Brid.) M. Fleisch. *ex* Broth., Nat. Pflanzenfam. (ed. 2) 11: 199. 1925. *Homaliodendron decompositum* (Brid.) K. Wagner, Bryologist 55: 144. 1952. Protologue. [Caribbean] In Hispaniolâ. Clar. Desvaux communicavit.

Neckera scalpellifolia Mitt., J. Proc. Linn. Soc., Bot., Suppl. 1: 119. 1859. *Homalia scalpellifolia* (Mitt.) Bosch & Sande Lac., Bryol. Jav. 2: 60. 1863. *Porotrichum scalpellifolium* (Mitt.) Mitt., Trans. Linn. Soc. London, Bot. 3: 175. 1891. *Homaliodendron scalpellifolium* (Mitt.) M. Fleisch., Hedwigia 45: 75. 1906. Protologue. Hab. In Ceylon, *Gardner.* Etiam e Java accepi sub nom. *N. Javanicae* (see Enroth 1989).

Neckera mohriana Müll. Hal., Linnaea 38: 646. 1874. *Homalia mohriana* (Müll. Hal.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 298. 1877. *Homalia mohrii* Müll. Hal. *ex* Kindb., Enum. Bryin. Exot. 16. 1888, illegitimate name, error for *Homalia mohriana*. *Homaliodendron mohrianum* (Müll. Hal.) M. Fleisch., Hedwigia 45: 77. 1906. Protologue. Patria. Mexico, Mirador, ad corticem arborum in sylvis umbrosis, 4–4500 pedes alta: *C. Mohr*.

Porotrichum grandidens Müll. Hal., Hedwigia 37: 243. 1898. Protologue. Habitatio. Haiti, Bois de Furcy, 1515 m alt.: *Picarda* lg. Aug. 1891. Hb. Berolin.

Porotrichum grandidens var. *domingense* Müll. Hal., Hedwigia 37: 243. 1898. Protologue. [Hispaniola] Habitatio. St. Domingo, prope Valle nuevo ad arbores sylvarum, 1900 m alt., Majo 1887: v. *Eggers* in Hb. Krug et Urban.

Plants medium-sized to robust, 3–10 cm high, stipitate-frondose, flattened, forming pale green or yellowish green, lax tufts. Stolons creeping; rhizoids smooth, reddish brown, densely present on stolons and at the base of stipitate stems; leaves appressed, widely spaced, evenly foliate, triangular-lanceolate. Secondary stems erect, stipitate, irregularly bi- or tripinnate, complanate-foliate, at times flagellate-attenuate; secondary stems in cross section with sclerodermis of 3–6 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia narrowly foliose to filamentous. Stipe leaves erect-spreading from an appressed base, evenly foliate, triangular to oblong-triangular, 1.5–2.0 mm long, broadly acuminate; margins entire to subentire below, serrate above; costae single, ending above midleaf. Stem leaves 2–4 mm long, branch leaves 1.0–1.5 mm long, both flattened, spreading to wide-spreading, smooth when dry or wet, broadly oblong-ovate, oblong-ligulate, obovate, or oblong-spathulate, asymmetric, broadly rounded and coarsely toothed at apex, teeth consisting of 4–8 rows of rhomboid cells, terminal tooth usually longer than the lower teeth, narrowly decurrent, straight at the insertion; margins inflexed on one side below, entire to subentire below; costae slender, often spurred below, tapering and occasionally forked above, reaching 1/2–2/3 the leaf length; cells smooth, apical cells rounded-rhomboid to hexagonal, or shortly fusiform, 12–20 µm long, firm- to thick-walled, occasionally porose, median cells oblong-rhomboidal, linear-rhomboidal, or long-rectangular, 30–50 µm long, thick-walled, porose, basal

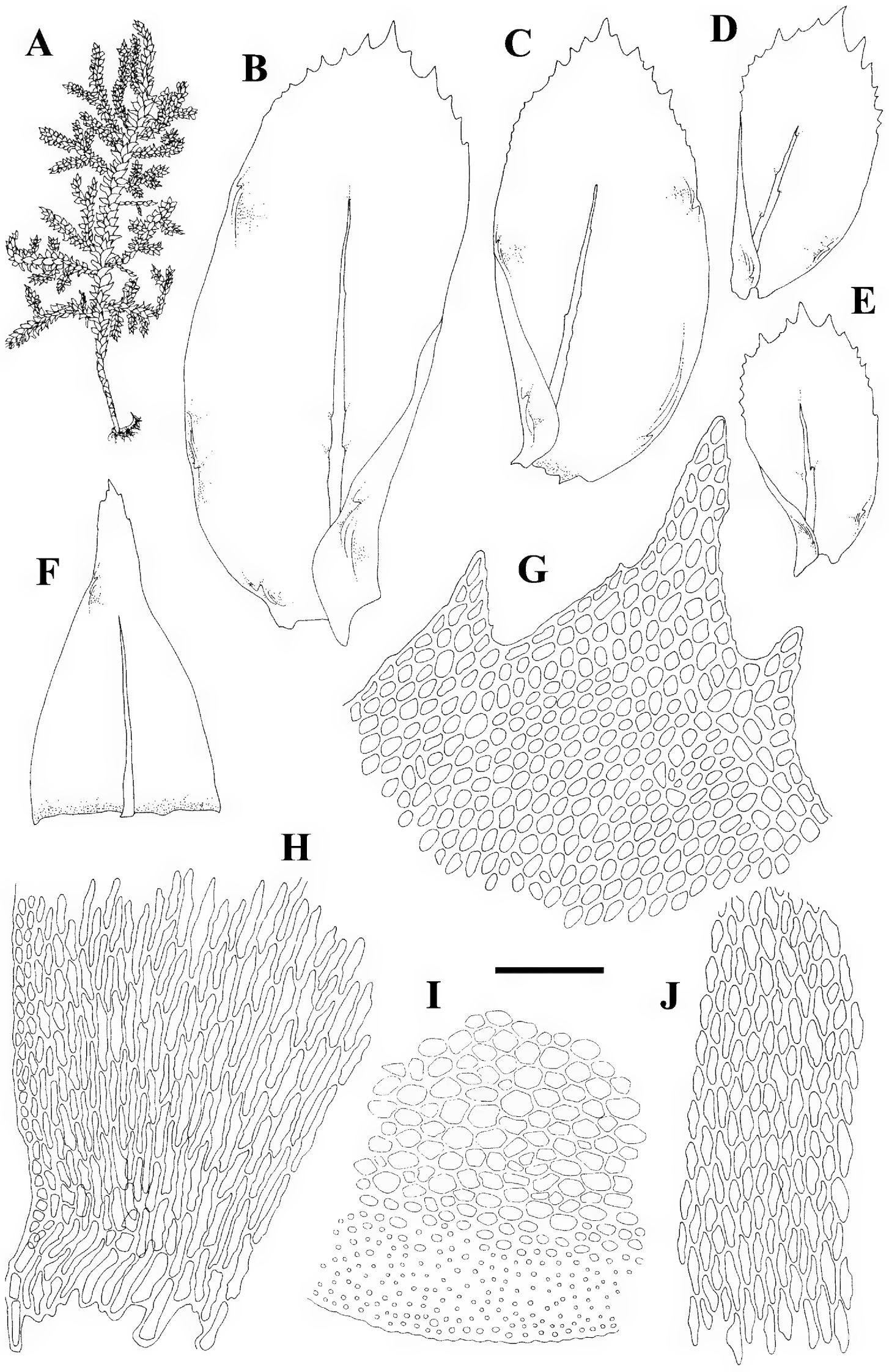
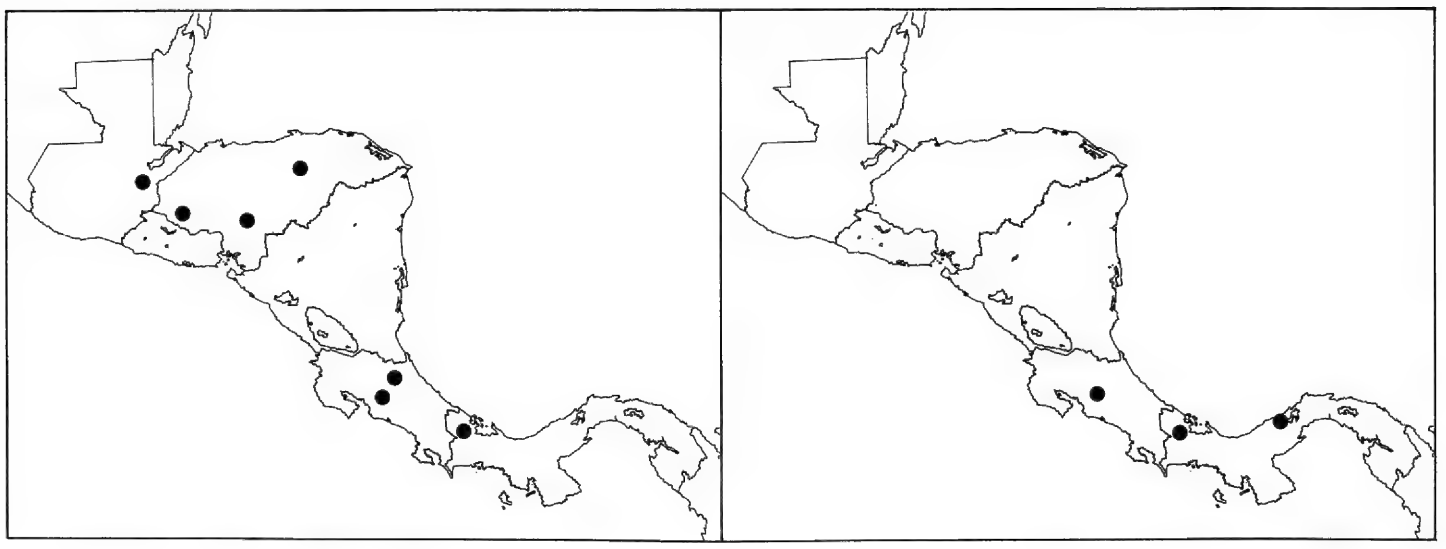


Figure 88. *Homaliodendron flabellatum*. A. Habit. B & C. Stem leaves. D & E. Branch leaves. F. Stipe leaf. G. Leaf apex. H. Basal and alar cells. I. Stem in cross section. J. Median leaf cells. Scale in mm: bar = 0.06 (G, H, J); bar = 0.08 (I); bar = 0.5 (B–F); bar = 12.7 (A). All figure parts from *Allen 11333*.



Homaliodendron flabellatum *Homaliodendron piniforme*

juxtacostal cells linear-fusiform, thick- to firm-walled, porose, basal marginal cells rectangular to subquadrate; alar cells rectangular to oblong-rectangular, weakly differentiated, cells across the insertions porose. Asexual reproduction by microphyllous branches. Dioicous. Sporophyte unknown in the Neotropics, description from Ninh (1984) and Enroth (1989). Perichaetia to 2 mm long; leaves ovate at base, ligulate to long lanceolate and spreading above, dentate at apex. Setae 1.5–4.5 mm long, smooth throughout or smooth below and mammillose above. Capsules ovoid-cylindrical, 1.5–3.0 mm long; exothecial cells near mouth subquadrate, thick-walled, short-rectangular, thick-walled below; stomata on neck; opercula conic, obliquely short-rostrate; annuli weakly differentiated; peristome diplolepideous; exostome teeth linear-lanceolate, 0.6–0.7 mm long, papillose throughout; endostome basal membranes short, segments similar to exostome teeth in shape and size, cilia not noted. Spores 14–20 µm, papillose. Calyptrae cucullate, sparsely hairy, smooth.

Illustrations. Smith (1808, Pl. 23 2); Hooker (1818, Pl. 69, as *Neckera dendroides*); Dozy and Molkenboer (1863, Pls. 178 & 180); Fleischer (1908, Fig. 158, as *Homaliodendron javanicum*); Bartram (1933a, Fig. 134); Bartram (1939, Pl. 18 306); Bartram (1949, Fig. 126 C–D); Gangulee (1976, Fig. 703, as *Homaliodendron ligulaefolium*; Fig. 704, as *Homaliodendron scalpellifolium*); Ninh (1984, Fig. 10, as *Homaliodendron ligulaefolium*; Fig. 11, as *Homaliodendron scalpellifolium*; Fig. 15, as *Homaliodendron squarrulosum*; Figs. 17–19); Enroth (1989, Figs. 8 & 9); Noguchi (1989, Fig. 316, as *H. scalpellifolium*); Sharp *et al.* (1994, Fig. 562); Duarte Bello (1997, Pl. 210); Buck (1998, Pl. 45 10–19); Gradstein *et al.* (2001, Fig. 216 A–D). Figure 88.

Habitat. On bark, trunks, and branches of trees and on vines; 1415–3000 m.

Distribution in Central America. GUATEMALA. Zacapa: *Steyermark 43229* (F, FH, MO, NY). HONDURAS. Francisco Morazán: *Richards 3537a* (F); Lempira: *Allen 11333* (MO); Olancho: *Allen 12832* (MO). COSTA RICA. Heredia: *Hatheway & Hatheway 1713* (US); San José: *Griffin & Morales B 107* (F, MO, NY). PANAMA. Bocas del Toro: *Gómez et al. 21958* (MO).

World range: Mexico; Central America; Caribbean; Western Indian Ocean; China, Eastern Asia; Indian Subcontinent, Indo-China, Malesia; Australia; Southwestern and North-Central Pacific.

Homaliodendron flabellatum is a medium-sized to robust species with strongly stipitate secondary stems that arise from well-developed primary stems or stolons. In Central America the species is found only at high elevations on tree trunks and vines. In other parts of its range, however, it occurs on rocks. The stems of *H. flabellatum* are complanate-foliate and irregularly bi- or tripinnately branched. Its leaves are smooth whether wet or dry, asymmetric, broadly inflexed on one side, and coarsely, deeply dentate at the apex. The remarkable marginal teeth in *H. flabellatum* are multicellular and sometimes consist of eight rows of cells. The branch leaves are often obovate or oblong-spathulate. The costae in *H. flabellatum* are slender, tapered to the apex, and are often spurred below. Its leaf cells are smooth, often porose below, and rounded-rhomboidal to hexagonal above. The sporophytes of

H. flabellatum are unknown in Central America; the species appears to reproduce asexually by means of deciduous, flagelliform branchlets.

Homaliodendron piniforme is a smaller species than *H. flabellatum*; it also differs in having serrate leaf margins. The serrations on the leaf margins in *H. piniforme* are unicellular. In the field *H. flabellatum* can be confused with robust species of *Porotrichum*. The Central American species of that genus, however, differ from *H. flabellatum* in having a stem central strand, fusiform upper leaf cells, and serrulate to serrate leaf margins.

The type collection of *Hookeria flabellata* was sent to Smith by Dickson and attributed to the West Indies. Dixon (1930) indicated a duplicate of the type in the Hooker herbarium (now at BM) bears the additional information "St. Vincent's ?", and so questioned the origin of the specimen. In this respect Mitten's (1875) comments on Dickson's localities are germane: "Dickson obtained specimens of mosses from the voyages of trading vessels, and localities were then not so precisely mentioned, so that any gathered during the voyage were liable to be reported as if gathered in the country the vessel had returned from; and there are some of the species which Dickson in this manner procured, of which the native country has yet to be discovered."

2. *Homaliodendron piniforme* (Brid.) Enroth, Nova Hedwigia 51: 55. 1990. *Pilotrichum piniforme* Brid., Bryol. Univ. 2: 260. 1827. *Hypnum piniforme* (Brid.) Müll. Hal., Syn. Musc. Frond. 2: 228. 1851. *Porotrichum piniforme* (Brid.) Mitt., J. Linn. Soc., Bot. 12: 465. 1869. *Thamnium piniforme* (Brid.) Kindb., Hedwigia 41: 238. 1902. *Pinnatella piniformis* (Brid.) M. Fleisch., Hedwigia 45: 81. 1906. Protologue. In insulâ Guadelupâ ad arbores habitat. Quis detexerit ignoramus. Herb. Cand.

Plants medium-sized to robust, 2–8 cm high, stipitate-frondose, flattened, forming pale green or yellowish green, lax tufts. Stolons creeping; rhizoids smooth, reddish brown, densely present on stolons and at the base of stipitate stems; leaves appressed, widely spaced, evenly foliate, triangular-lanceolate. Secondary stems erect, stipitate, irregularly bi- or tripinnate, complanate-foliate, at times flagellate-attenuate; secondary stems in cross section with sclerodermis of 3–6 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia narrowly foliose to filamentous. Stipe leaves erect-appressed when dry, somewhat spreading from an appressed base when wet, evenly foliate, triangular to oblong-triangular, 1.0–1.5 mm long, acuminate to broadly acuminate; margins plane, entire to lightly serrulate; costae single or double, ending above midleaf. Stem leaves 1.0–1.5 mm long, branch leaves 0.5–1.0 mm long, both strongly flattened, spreading to wide-spreading, more or less plicate when dry, smooth when wet, oblong-ovate, asymmetric, short-acute to short-acuminate, narrowly decurrent, straight at the insertion; margins subentire, serrulate, or serrate, inflexed on one side below, otherwise plane; costae often spurred below, strong throughout, reaching 1/2–2/3 the leaf length; cells smooth, apical cells oval, rounded-rhomboid, or elliptic, 6–14 µm long, firm- to thick-walled, not porose, median cells long-oval to long-rhomboidal, 12–18 µm long, firm-walled, not porose; basal cells and median cells near the costa long-rectangular, 24–30 µm long, thick-walled, often porose; alar cells rectangular to oblong-rectangular, weakly differentiated, cells across the insertions porose. Asexual propagula not seen. Dioicous. Perigonia not seen. Perichaetial lateral on secondary stems and branches, 1.5–2.0 mm high; inner perichaetial leaves erect and sheathing at base, wide-spreading to recurved above, 1.0–1.5 mm long; apices long, acuminate; margins serrulate above; costae single and faint or absent; cells elongate-fusiform, very thick-walled and porose. Sporophytes known only from a single Cameroon collection, description from Enroth (1990). Setae 3.6–5.5 mm long, straight, yellowish. Capsules ovate to ovate-oblong, 1.8–2.4 mm long; exostome teeth yellowish, dorsal (outer) surface cross-striolate at base; endostome basal membranes high, segments, cilia, spores, and calyptrae not seen.

Illustrations. Dusén (1895, p. 39 a–g, as *Porotrichum chalaropteris*, p. 40 a–g, p. 41 a–f, Pl. 1 1, Pl. 5 1–3); Florschütz-de Waard (1986, Fig. 109); Enroth (1990, Fig. 1); Sharp *et al.* (1994, Fig. 567); Buck (1998, Pl. 45 1–9); Buck (2003, Fig. 104). Figure 89.

Habitat. At base of trees and hanging on shrubs; 450–950 m.

Distribution in Central America. COSTA RICA. San José: *Holz & Schäfer-Verwimp CR 99-1321* (MO). PANAMA. Bocas del Toro: *Allen 5637* (MO); Colón: *Crosby 10388* (MO).

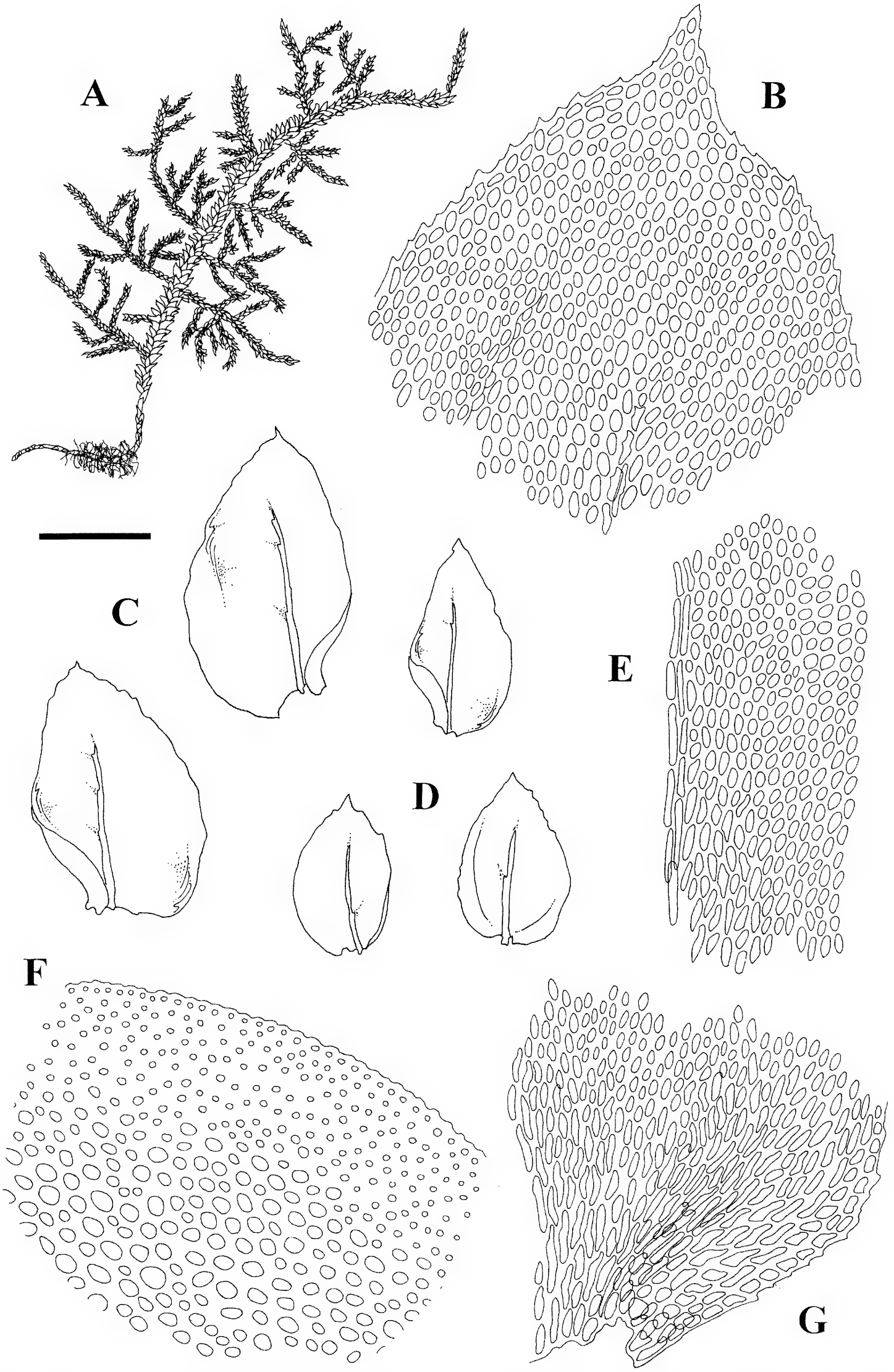


Figure 89. *Homaliodendron piniforme*. A. Habit. B. Leaf apex. C. Stem leaves. D. Branch leaves. E. Median leaf cells near costa. F. Stem in cross section. G. Basal and alar cells. Scale in mm: bar = 0.06 (B, E–G); bar = 0.4 (C, D); bar = 8.0 (A). All figure parts from *Allen 23700*.

World range: Mexico; Central America; Caribbean; Western and Northern South America, Brazil; West, West-Central, and East Tropical Africa, Western Indian Ocean.

Homaliodendron piniforme is a medium-sized to robust moss, with a complex morphology of creeping primary stems and erect secondary stems. The secondary stems can be long and strongly stipitate or fairly short and non-stipitate. Remarkably, stipitate and non-stipitate secondary stems can sometimes be found on the same primary stem. Often its secondary stems, and sometimes its branches, end in filiform attenuations or stolons. These different structures can be morphologically distinct, intergrade one into another, or they can abruptly transform from one structure to another. The secondary stems and branches of *H. piniforme* are complanate-foliate, with asymmetric, oblong-ovate leaves that are short-acute to short-acuminate, and usually serrate above. Its leaf margins are broadly inflexed on one side below, and the often spurred costae are strong throughout, usually reaching two thirds the leaf length. Its upper leaf cells are predominantly oval or rounded-rhomboid (with occasional elliptic cells here and there) and usually thick-walled. At base, especially near the costa, the cells are long-rectangular and often porose. The alar cells are weakly differentiated, of only a few rectangular to oblong-rectangular cells.

Homaliodendron flabellatum is generally considered to be a larger species than *H. piniforme*; however, the species have a similar size range. As noted by Buck (1998) and Enroth (1990), the upper leaf cell size and shape in both species is remarkably similar. *Homaliodendron flabellatum* is best distinguished from *H. piniforme* by its strongly toothed upper leaf margins. Sastre (1987) placed *H. piniforme* in *Porotrichum* on the basis of the shape of its upper leaf cells and serrate leaf margins. Enroth (1990), however, emphasized the absence of a stem central strand and its short setae in placing the species in *Homaliodendron* rather than *Porotrichum*. Fleischer (1906) placed *H. piniforme* in *Pinnatella*. According to Enroth (1994a), *Pinnatella* differs from *Homaliodendron* in having stipe leaves that are spreading to squarrose, with recurved margins, less strongly complanate and less asymmetric stem and branch leaves, generally longer and stronger costae, the presence of differentiated marginal leaf cells, and an intramarginal limbidium in the leaves. Enroth (1994a) listed the "mostly smooth setae" of *Homaliodendron* as another feature separating it from *Pinnatella*, but the character is fully overlapping since *Pinnatella*, which usually has species with mammillose setae, also has some species with smooth setae (Enroth 1994a).

3. *Isodrepanium* (Mitt.) E. Britton *in* E. Britton & R. S. Williams, Torreya 14: 27. 1914. *Lepidopilum* (Brid.) Brid. sect. *Isodrepanium* Mitt., J. Linn. Soc., Bot. 12: 366. 1869. *Homalia* Brid. sect. *Isodrepanium* (Mitt.) Müll. Hal., Hedwigia 37: 266. 1898.

Plants medium-sized to large, flattened, pale green to yellowish green, at times yellowish red, glossy. Primary stems creeping, occasionally pendent; rhizoids smooth, reddish brown, densely present on stolons and on secondary stems and branches when in contact with substrate; leaves appressed to spreading, sigmoid-oblong, evenly foliate. Secondary stems erect, horizontal or pendent, not stipitate, irregularly branched, complanate-foliate, at times flagellate-attenuate; secondary stems in cross section with sclerodermis, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia foliose. Secondary stems and branches complanate-foliate; leaves spreading to wide-spreading, smooth when dry or wet, cultriform to sigmoid-oblong, short-acuminate, not decurrent, rounded to the insertion; margins serrulate above, subentire below, inflexed on one side below; costae usually faint, very short and double; cells smooth, apical cells long-hexagonal to long fusiform, firm- to thick-walled, porose; basal cells linear-fusiform, thick-walled, porose; alar cells not or very weakly differentiated, cells across the insertions yellow. Asexual reproduction occasionally by deciduous leaves or filiform, axillary branchlets. Dioicous. Setae elongate. Capsules suberect to inclined, short-cylindric, symmetric; stomata on neck; opercula obliquely long-rostrate; annuli well developed; peristome diplolepideous; exostome teeth narrowly triangular, dorsal surface densely cross-striate below, coarsely papillose above, trabeculae and median lines well developed; endostome basal membranes high, segments broadly perforate, keeled, cilia rudimentary, 1–2. Calyptrae cucullate, smooth.

Isodrepanium is a genus of a single Neotropical species. The genus has strongly complanate-foliate stems, with leaves that are strongly asymmetric to cultriform. Its leaf cells are uniformly long-flexuose and porose throughout, and its alar cells are weakly developed. The single species of *Isodrepanium* was originally described in *Homalia*, and the two genera are gametophytically similar in having weakly costate, complanate leaves inserted in eight ranks (Florschütz-de Waard 1986; He 1997) with poorly developed alar cells and smooth, cucullate calyptrae. Furthermore, the genera have similar sporophytes: setae elongate; capsules suberect to inclined, short-cylindric; stomata present; opercula obliquely long-rostrate; annuli well developed; exostome densely cross-striate on dorsal (outer) surface; endostome with a high basal membrane and well-developed segments. Plants of *Homalia* are much more glossy than those of *Isodrepanium*, and they grow in strongly flattened mats. In addition, the oblong-ovate to oblong-spathulate leaves of *Homalia* are usually rounded-obtuse and have isodiametric to rounded or rhomboidal upper leaf cells.

The leaves of *Neckera* and *Isodrepanium* are somewhat similar in shape. However, many species of *Neckera* have undulate leaves, and they are never as strongly cultriform as those of *Isodrepanium*. The genus further differs from *Isodrepanium* in having short setae (capsules immersed to short-exserted) and a reduced, neckeroid peristome. *Isodrepanium* has sometimes been placed in the Hookeriaceae, probably because of a gametophytic similarity to the genus *Lepidopilum*. *Lepidopilum* differs from *Isodrepanium* in having thin-walled, non-porose leaf cells, often plicate and hairy mitrate calyptrae, and a hookeroid peristome.

The name *Isodrepanium* is combines the Greek *isos* (equal or like) with *drepano* (sickle-shaped), and refers to its distinctively shaped leaves.

Isodrepanium lentulum (Wilson) E. Britton *in* E. Britton & R. S. Williams, Torreya 14: 28. 1914. *Homalia lentula* Wilson, Ann. Mag. Nat. Hist. 20: 379. 1847, "*Omalia.*" *Neckera lentula* (Wilson) Broth., Nat. Pflanzenfam. I(3): 842. 1906. Protologue. [Jamaica] Hab. in arborum cortice? Port Royal; legit *G. M'Nab*, M.D. Type (see He 1997). Jamaica. Port Royal, in arborum cortice, *McNab s.n.* (BM, lectotype).

Hookeria membranacea Müll. Hal., Syn. Musc. Frond. 2: 200. 1851. *Lepidopilum membranaceum* (Müll. Hal.) Mitt., J. Linn. Soc., Bot. 12: 369. 1869. *Homalia membranacea* (Müll. Hal.) Müll. Hal., Hedwigia 37: 266. 1898. Protologue. Insula Trinidad Antillarum, monte Tocuche, ubi modo *H. Patrisiae* ramos tenues et folia arborum habitat: *Crüger* 1847. Sterilem legit.

Neckera falcifolia Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32(1): 184. 1893. Protologue. [Costa Rica] Montaña de Poás, massif de l'Iscasu, 2400 m. (*Pitt.*[*ier*] *5642*). Forêts du Rio Naranjo ([*Pittier*] *5702*).

Homalia angustifrons Müll. Hal., Bull. Herb. Boissier 5: 203. 1897. Protologue. Guatemala. Sine loco speciali quam linteum involucris serviens in Museo Zoolog. Florentino. HB. *Levier* 1893. Type (see He 1997). Guatemala. *Levier s.n.*, 1893 (FI, isotype).

Plants medium-sized to large, 2–15 cm long, flattened, pale green to yellowish green, at times yellowish red, glossy. Primary stems (stolons) creeping, occasionally pendent; rhizoids smooth, reddish brown, densely present on stolons and on secondary stems and branches when in contact with substrate; leaves appressed to spreading, sigmoid-oblong, evenly foliate, 0.8–1.5 mm long. Secondary stems erect, horizontal or pendent, not stipitate, irregularly branched, complanate-foliate, at times flagellate-attenuate; secondary stems in cross section with sclerodermis of 3–6 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia foliose. Secondary stem and branch complanate-foliate; leaves spreading to wide-spreading, smooth when dry or wet, cultriform to sigmoid-oblong, 1.5–2.5 mm long, asymmetric, short-acuminate, not decurrent, rounded to the insertion; margins serrulate above, subentire below, inflexed on one side below; costae usually faint, very short and double; cells smooth, apical cells long-hexagonal to long fusiform, 30–60 × 4–6 µm, firm- to thick-walled, porose; basal cells linear-fusiform, 60–80 × 4–6 µm, thick-walled, porose; alar cells not or very weakly differentiated, cells across the insertions yellow. Asexual reproduction occasionally by deciduous leaves or filiform, axillary branchlets. Dioicous. Perichaetial leaves oblong, sheathing at base, long-acuminate. Setae elongate, 2.5–4.0 cm, smooth, red. Capsules suberect to inclined, short-cylindric, symmetric, 1.5–2.0 mm long; exothecial cells not strongly differentiated at mouth, those below rounded, subquadrate to short-rectangular, firm- or thick-walled; stomata on neck; opercula obliquely long-rostrate, 0.8–1.2 mm long; annuli well de-

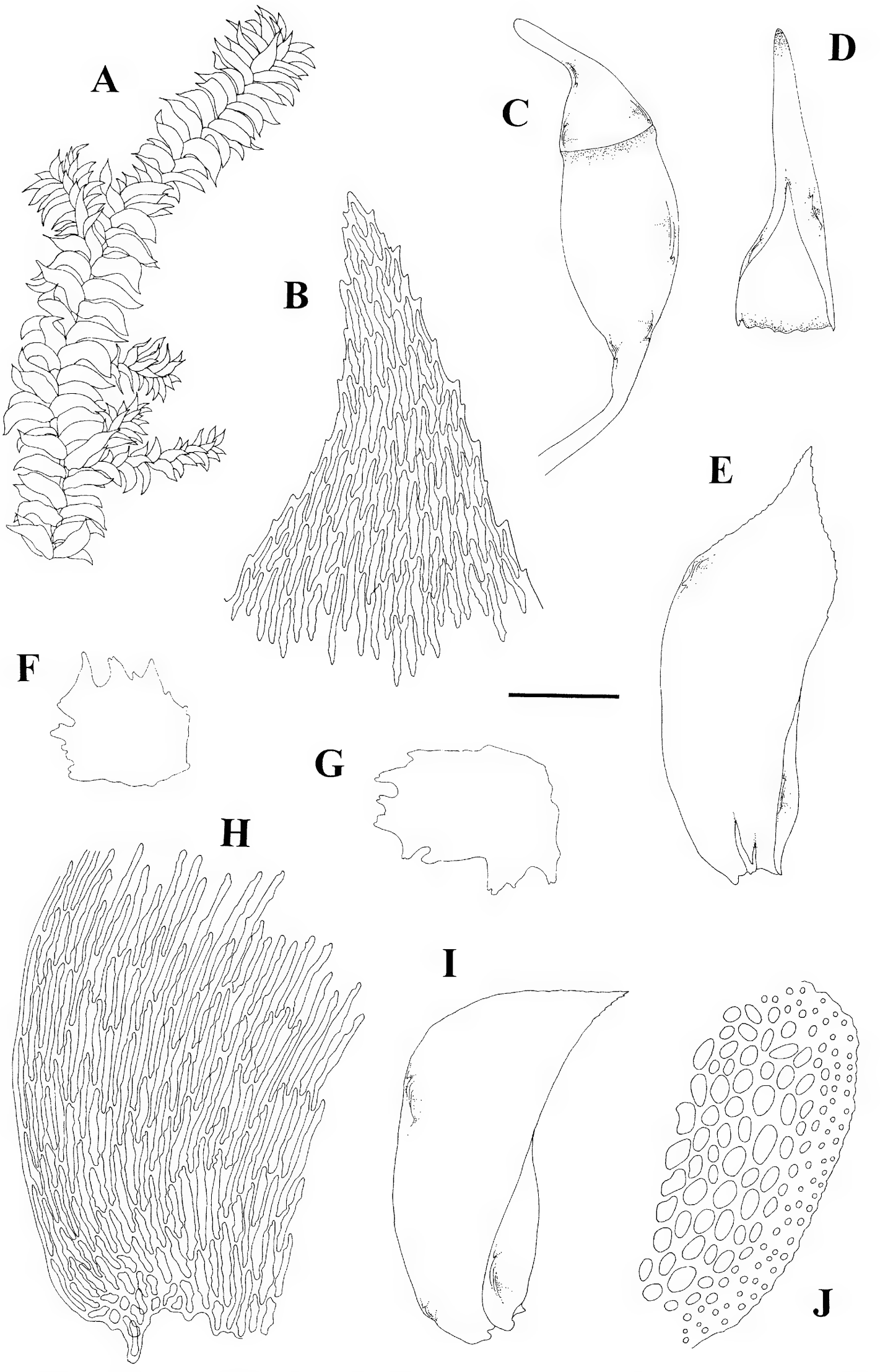
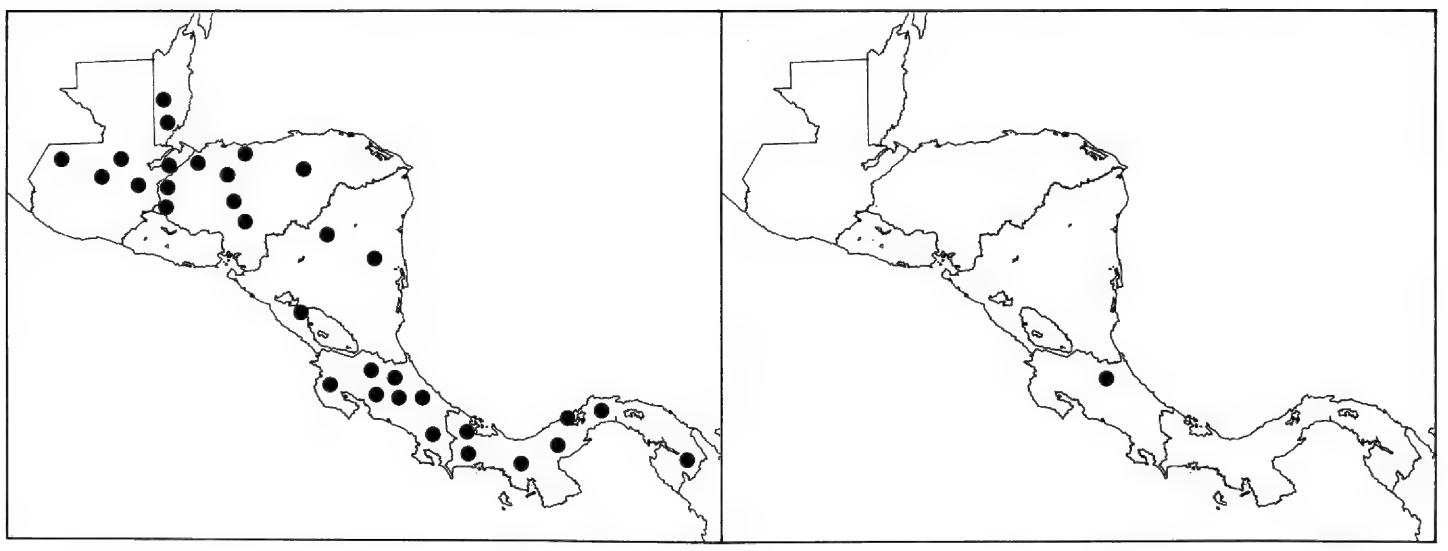


Figure 90. *Isodrepanium lentulum*. A. Habit. B. Leaf apex. C. Seta, capsule, and operculum. D. Calyptra. E & I. Leaves. F & G. Pseudoparaphyllia. H. Basal and alar cells. J. Stem in cross section. Scale in mm: bar = 0.04 (F, G); bar = 0.06 (B, H, J); bar = 0.6 (E, I); bar = 0.9 (C, D); bar = 4.0 (A). C, D from *Allen 15123*; all other figure parts from *Allen 14487*.



Isodrepanium lentulum *Neckera chilensis*

veloped, of a layer of enlarged, thick-walled, fragmenting cells; peristome diplolepideous; exostome teeth yellow to yellowish brown, narrowly triangular, 0.4–0.8 mm long, dorsal surface densely cross-striate below, coarsely papillose above, trabeculae and median lines well developed; endostome light yellow, lightly papillose throughout, basal membranes high, well developed, 0.1–0.2 mm long, segments subulate, 0.2–0.5 mm long, broadly perforate, keeled, cilia 1–2, rudimentary. Spores 16–22 µm, papillose. Calyptrae cucullate, smooth, to 2 mm long.

Illustrations. Britton and Williams (1914, Fig. 1); Bartram (1949, Fig. 141 D–G); Florschütz-de Waard (1986, Fig. 108); Sharp *et al.* (1994, Fig. 619); Churchill and Linares (1995, Fig. 130 a–e); Duarte Bello (1997, Pl. 211); Buck (1998, Pl. 41); Gradstein *et al.* (2001, Fig. 159 A–E); Buck (2003, Fig. 105). Figure 90.

Habitat. Pendent on tree trunks, branches, twigs, shrubs, prop roots, and vines, occasionally on rotten logs, on sticks, twigs, and leaf litter on forest floor; 200–2350 m.

Distribution in Central America. BELIZE. Cayo: *Allen* 15123 (MO); Toledo: *Allen 18743* (BRH, MO). GUATEMALA. Alta Verapaz: *Steyermark 44462* (F, FH); Baja Verapaz: *Sharp 5206* (F, FH, NY); Huehuetenango: *Steyermark 48859* (F, FH); Izabal: *Steyermark 41935a* (F, FH); Zacapa: *Steyermark 29853* (F, FH, NY). HONDURAS. Atlántida: *Allen 17513* (MO, TEFH); Comayagua: *Allen 13896* (MO); Copán: *Allen 17726* (MO, TEFH); Cortés: *Allen 14157* (MO); Francisco Morazán: *Allen 12396* (MO); Ocotepeque: *Allen 14487* (MO); Olancho: *Allen 12653* (MO); Yoro: *Allen 13635* (MO). NICARAGUA. Granada: *Croat 39146* (MO); Jinotega: *Stevens 11387* (HNMN, MO); Zelaya: *Stevens 7443A* (MO). COSTA RICA. Alajuela: *Brenes 19140* (F, FH, NY); Cartago; *Alfaro 62b* (F); Guanacaste: *Dauphin 2581* (MO); Heredia: *Standley & Valerio 52162* (FH, US); Limón: *Crosby 3679* (MO); Puntarenas: *Lyon 519* (MO); San José: *Griffin et al. 019950* (F, MO, NY, US). PANAMA. Bocas del Toro: *Allen 5778* (MO); Chiriquí: *Allen 5468* (MO); Coclé: *Crosby 4417* (MO); Colón: *Crosby 10470* (MO, PMA); Darién: *Allen 8876* (MO); Panamá: *Crosby 10085* (MO); Veraguas: *Crosby 10162* (MO, PMA).

World range: Mexico; Central America; Caribbean; Western and Northern South America, Brazil.

Although *Isodrepanium lentulum* occurs in a variety of habitats, it is essentially a corticolous species found on tree twigs, branches, trunks, and roots. It is morphologically plastic, with plants varying from unbranched to irregularly 1–2-pinnately branched. The stem leaves of *I. lentulum* are typically strongly complanate and cultriform, but the branch and pendent stem leaves can be weakly complanate and more or less ovate-lanceolate. The leaf cells of *I. lentulum* are uniformly long-fusiform, distinctly porose throughout, and the alar cells are not or very poorly developed. The leaf margins are serrulate above, and the costa is short and double. The sporophytes of *I. lentulum* are nearly identical to those of *Homalia glabella*: setae very long; capsules short-cylindric; annuli well developed; exostome teeth strongly cross-striate on the lower dorsal (outer) surface; endostome well developed, basal membrane high, cilia present.

Plants with well-developed stem leaves are superficially similar to *Phyllodrepanium falcifolium* (Schwägr.) Crosby. That species differs from *I. lentulum* in having leaves with strong, single costae, terminal clusters of filiform propagula, and shorter, quadrate to rhombic upper leaf cells. In overall appearance, leaf shape, and costal form *I. lentulum* could be confused with some *Lepidopilum* species. In *Lepidopilum*, however, the leaf cells are lax, thin-walled, and not porose.

4. ***Neckera*** Hedw., Sp. Musc. Frond. 200. 1801, conserved name, not *Neckeria* Scop., Intr. Hist. Nat. 313. 1777 [Papaveraceae], rejected name.

Eleutera P. Beauv., Mag. Encycl. 5. 1804, invalid name, lacks a description.
Eleuteria P. Beauv., Prodr. Aethéogam. 56. 1805, invalid name, lacks a description.
Cryptopodia Röhl., Deutschl. Fl. (ed. 2), Kryptog. Gew. 3(1): 82. 1813. *Neckera* Hedw. sect. *Cryptopodia* (Röhl.) Limpr. *in* Rabenh., Deutschl. Krypt.-Fl., ed. 2, 4(2): 698. 1894.
Rhystophyllum Ehrh. *ex* E. Britton, Bryologist 8: 5. 1904.

Plants medium-sized to large, in usually flattened, pale green to yellowish green masses. Primary stems creeping; rhizoids smooth, reddish brown, not or irregularly branched, densely present on stolons and secondary stems and branches when in contact with substrate; leaves erect, small. Secondary stems erect, horizontal or pendent, not stipitate, irregularly branched, complanate-foliate; secondary stems in cross section with sclerodermis and enlarged, thick- to firm-walled cortical cells, central strand absent; paraphyllia present or absent; pseudoparaphyllia foliose. Secondary stem and branch leaves erect-spreading or spreading, undulate (plane in species outside the region), oblong-ovate, oblong-lanceolate, or ovate-lanceolate, symmetric or asymmetric, acute to broadly acute, long- or short-decurrent, subauriculate, rounded or straight to the insertion; margins subentire, serrulate or denticulate, broadly inflexed on one side below, plane or narrowly recurved on other side; costae faint, short and double with one fork usually longer than the other (long and single outside the region); cells smooth, apical cells hexagonal, rhomboidal or fusiform, firm- to thick-walled; basal cells linear-fusiform, thick-walled, often porose; alar cells hyaline or reddish yellow, not or moderately developed, cells across the insertions yellow. Autoicous. Setae smooth, yellow to yellow red. Capsules immersed or exserted, erect, cylindric, symmetric; exothecial cells not strongly differentiated at mouth, those below short-rectangular, firm- or thick-walled; stomata present or absent; opercula conic-rostrate; peristome diplolepideous; exostome teeth whitish yellow, dorsal (outer) surface cross-striate at base, trabeculae and median lines faintly developed, ventral (inner) surface smooth to weakly papillose, trabeculae well developed; endostome light yellow, lightly papillose, basal membranes variously developed, segments perforate, not keeled, more strongly thickened on the ventral (inner) surface than on the dorsal (outer) surface, cilia rudimentary or absent. Spores papillose. Calyptrae cucullate, naked, smooth.

Neckera is a genus of 71 species (Crosby *et al.* 2000) found throughout the world. It has been regionally revised for many areas—eastern North America (Crum & Anderson 1981), Pacific Northwest (Lawton 1971), Mexico (Smith 1994), Neotropics (Sastre 1987), Great Britain (Smith 2004), Belarus (Rykovsky & Maslovksy 2004), Middle Russia (Ignatov & Ignatova 2003), Karelia (Abramov & Volkova 1998), Japan (Noguchi 1989), tropical Africa (De Sloover 1977), South Africa (Magill & Rooy 1998), eastern India (Gangulee 1976), Tibet (Li 1985), southern Australia (Scott & Stone 1976), and New Zealand (Beever *et al.* 1992)—and as a result 42 of the species are well known. Brotherus (1925) provided the last comprehensive treatment of *Neckera.*

The genus is found predominantly as an epiphyte, but it also occurs on rocks and boulders. In Central America it is found only at high elevations. Gametophytically, *Neckera* is characterized by its often pendent habit and complanate-foliate stems that lack a central strand. The presence or absence of paraphyllia is a widely variable feature of *Neckera.* In some species they are abundantly present, in others apparently absent, and in still others at times either present or absent. The relative abundance of paraphyllia is also a variable feature in many *Neckera* species, and the presence of paraphyllia in some species appears to be correlated with the presence of perichaetia and to a lesser degree perigonia. The leaves in *Neckera* are usually oblong-lanceolate or ovate-lanceolate, asymmetric, acute to obtuse, and with the margins broadly inflexed on one side below. Its leaf cells are smooth and rhombic

to fusiform at the apex. Although many *Neckera* species have undulate leaves, there a number of species with plane leaves. The costae in *Neckera* are considerably variable between species; some characteristically have short, faint, double costae, while in others they are long and single. While the calyptrae in *Neckera* are typically cucullate, at times they are mitrate. The capsules of *Neckera* can be immersed or exserted, they are erect, cylindric, and they have weakly developed annuli. Stomata can be present or absent. The genus has a neckeroid peristome: narrow exostome teeth that are typically cross-striate at the very base on the dorsal surface and an endostome with low basal membranes, narrow, perforate, but not keeled segments, and cilia absent to rudimentary. Enroth (1994b) regarded the *Neckera* gametophyte and sporophyte to be evolutionarily advanced within the Neckeraceae.

The name *Neckera* was given in honor of Noël Martin Joseph de Necker (25 December 1730–1793), a French-born botanist and bryologist. He later was "kurpfalzischer Botaniker" at Mannheim (Stafleu & Cowan 1981; Frahm & Eggers 2001). Necker was an opponent of Hedwig's views on the sexuality of mosses (Crum & Anderson 1981).

1. Capsules immersed 2
1. Capsules exserted 3

2. Stomata absent; endostomial segments not thickened at the trabeculae; basal leaf margins often narrowly recurved; paraphyllia usually abundant and often more than 0.5 mm long . . . . . 2. *N. ehrenbergii*
2. Stomata present; endostomial segments nodose or occasionally appendiculate; basal leaf margins plane; paraphyllia sparse or absent and usually less than 0.5 mm long . . . . . 3. *N. scabridens*

3. Leaves mostly wide-spreading; non-inflexed side of leaves long-decurrent, straight to the insertions; alar cells 1–3, mostly hyaline; setae 2.0–2.5 mm long; exostome teeth to 0.5 mm long . . . . . 4. *N. urnigera*
3. Leaves mostly erect-spreading; non-inflexed side of leaves short-decurrent, subauriculate or rounded to the insertions; alar cells 6–10, reddish yellow; setae 2–3 mm long; exostome teeth to 1.0 mm long . . . . . 1. *N. chilensis*

1. *Neckera chilensis* Schimp., Ann. Sci. Nat., Bot. sér. 2, 6: 147. 1836. Protologue. [Chile] Hab. ad arbores cum *Neckera intermedia* Schw., in montosis Chiles (*Bertero*). Types (see Sastre 1987). BM, NY, isotypes.

Neckera jamesonii Taylor, London J. Bot. 5: 59. 1846. Protologue. [Ecuador] On the Quitinian Andes, *Prof. William Jameson*, 1845. Types (see Sastre 1987). FH, holotype; NY, isotype.

Neckera novae-granadae Müll. Hal., Bot. Zeitung (Berlin) 15: 581. 1857. Protologue. [Colombia] Nova Granada, prov. Rio Hacha, Sierra Nevada, Taquinaar, alt. 8000 pedum: *L. Schlim* in Collect. Linden *No. 871*. Types (see Sastre 1987). G, lectotype; NY, isolectotype.

Plants medium-sized to large, 5–15 cm long, in usually flattened, pale green to yellowish green masses. Primary stems (stolons) creeping; rhizoids smooth, reddish brown, not or irregularly branched, densely present on stolons and on secondary stems and branches when in contact with substrate; leaves erect, obovate to ovate-triangular, evenly foliate, 1–1.5 mm long. Secondary stems erect, horizontal or pendent, not stipitate, irregularly branched, complanate-foliate; secondary stems in cross section with sclerodermis of 3–4 rows of small, thick-walled cells, cortical cells enlarged, thick- to firm-walled, central strand absent; paraphyllia present or absent, uniseriate, less than 0.5 mm long; pseudoparaphyllia foliose. Secondary stems and branches complanate-foliate; leaves erect-spreading, occasionally spreading, undulate, oblong-lanceolate to ovate-lanceolate, 2.0–3.5 mm long, symmetric or asymmetric, acute, short-decurrent and subauriculate or rounded to the insertion; margins subentire to serrulate, broadly inflexed on one side below, plane or sometimes narrowly recurved on other side; costae faint, short and double with one fork usually longer than the other; cells smooth, apical cells rhomboidal or long fusiform, 26–42 × 4–6 µm, firm- to thick-walled; basal cells linear-fusiform, 50–80 × 4–8 µm, thick-walled, often porose; alar cells reddish yellow, of 6–10 subquadrate to subrectangular cells, cells across the insertions yellow. Autoicous. Perichaetial leaves oblong-lanceolate, 2–3 mm long; costae short and double or absent. Setae 2–3 mm, smooth, yellow to yellow

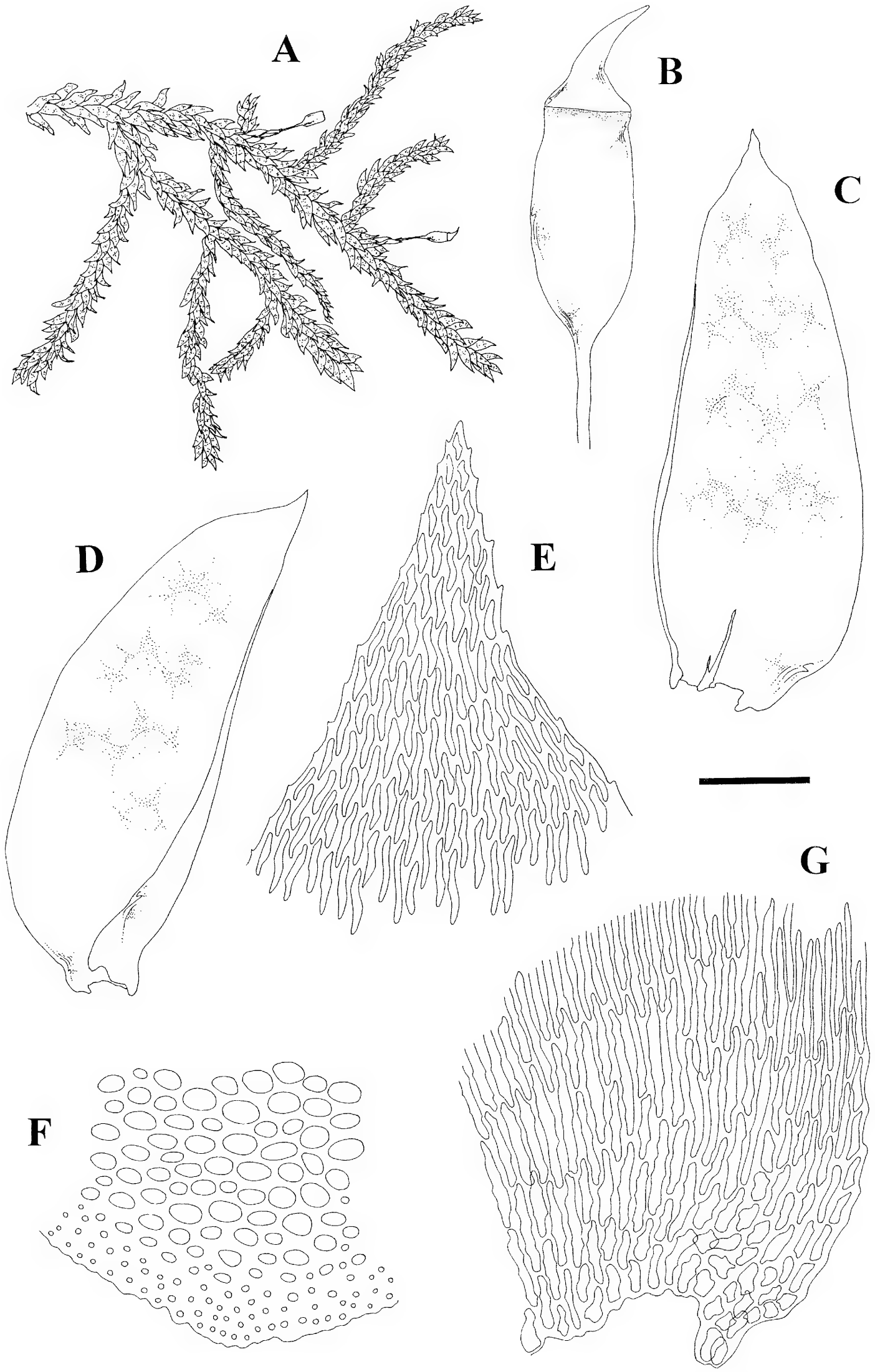


Figure 91. *Neckera chilensis*. A. Habit. B. Seta, capsule, and operculum. C & D. Leaves. E. Leaf apex. F. Stem in cross section. G. Basal and alar cells. Scale in mm: bar = 0.06 (E–G); bar = 0.5 (C, D); bar = 0.9 (B); bar = 8.0 (A). All figure parts from *Standley & Valerio 3689*.

red. Capsules exserted, erect, cylindric, symmetric, 1.5–2.0 mm long; exothecial cells not strongly differentiated at mouth, those below short-rectangular, firm- or thick-walled; stomata on capsule base; opercula conic-rostrate, 1 mm long; annuli rudimentary, of several layers of thin-walled, persistent cells; peristome diplolepideous; exostome teeth whitish yellow, linear, 1 mm long, dorsal (outer) surface cross-striate at base, vertically striate at middle, papillose above, trabeculae and median line faintly developed, ventral (inner) surface smooth to weakly papillose, trabeculae well developed; endostome light yellow, lightly papillose, basal membranes well developed, 0.07 mm high, segments 0.75 mm long, perforate, not keeled, papillose to lightly striate, more strongly thickened on the ventral (inner) surface than on the dorsal (outer) surface, cilia rudimentary or absent. Spores 30–34 μm, densely papillose. Calyptrae cucullate, naked, smooth, 2.0 mm long.

Illustrations. Churchill and Linares (1995, Fig. 130 f–i). Figure 91.

Habitat. On tree trunks; 2600–3000 m.

Distribution in Central America. COSTA RICA. Heredia: *Griffin et al. D219* (F, MO); San José: *Cryptogam Exsiccatae editae a Museo Hist. Natur. Vindobonensi 3689* [*Standley & Valerio 43547*] (F, FH, MO, US).

World range: Central America; Western, Northern, and Southern South America.

Neckera chilensis is a medium-sized to large moss known in Central America from only two high elevation localities in Costa Rica. Sastre (1987) considered it a páramo or subpáramo species. It has complanate-foliate stems with paraphyllia absent or weakly present, and distinctly undulate, ovate- to oblong-lanceolate leaves that can be symmetric or asymmetric. The leaves are mostly erect-spreading when dry, but this is a variable feature of the species, and single collections often have some leaves that are spreading when dry. The leaves are typically narrowly acute, with margins broadly inflexed on one side and either narrowly recurved or plane on the other side. On the non-inflexed side the leaves are short-decurrent and subauriculate or rounded to the insertions. The alar cells on this side of the leaves are dark red to reddish yellow and consist of 6–10 subquadrate to subrectangular, porose cells. *Neckera chilensis* has exserted, stomatose capsules. Its peristome is well developed with long, linear exostome teeth that are horizontally striate at base but vertically striate at the middle, and an endostome that has a relatively well-developed basal membrane, long segments, and often rudimentary, stub-like cilia.

Neckera urnigera is the only other Central American species of *Neckera* with exserted capsules. The two species are very similar and have been confused in the past; many herbarium specimens are misnamed. *Neckera urnigera* differs somewhat from *N. chilensis* in having spreading rather than erect-spreading leaves. This feature, however, is so variable in both species that it cannot be used to reliably separate the two species. Sastre (1987) considered *N. urnigera* to differ from *N. chilensis* in having equal-sized stem and branch leaves. This distinction is also unreliable in distinguishing them. The leaves of the two species consistently differ in their alar regions. In *N. urnigera* the leaves on the non-inflexed side are long-decurrent, straight to the insertions, and they have 1–3, mostly hyaline, subrectangular alar cells. Furthermore, the setae of *N. urnigera* are somewhat shorter than those of *N. chilensis* (2.0–2.5 mm vs. 2–3 mm long), and the exostome teeth are shorter (0.5 mm vs. 1.0 mm long).

Wijk *et al.* (1964) cite "Schimper *ex* Montagne" as the authors of this species, and this citation has been followed by most recent authors. Montagne, however, had nothing to do with the publication of the species.

2. *Neckera ehrenbergii* Müll. Hal., Syn. Musc. Frond. 2: 51. 1850. Protologue. Mexico. *C. Ehrenberg*. Types (see Sastre 1987). BM, lectotype; NY, isolectotype.

Neckera hornschuchiana Müll. Hal., Syn. Musc. Frond. 2: 51. 1850. Protologue. Mexico. *Deppe et Schiede*. Types (see Sastre 1987). BM, lectotype.

Neckera chlorocaulis Müll. Hal., Syn. Musc. Frond. 2: 663. 1851. Protologue. [Mexico] Prov. Mechoacan, Cerro San Andres, 1849. m Martii v. *Chrismar* legit.

Plants medium-sized to large, 4–12 cm long, in usually flattened, pale green to yellowish green, often pendent masses. Primary stems (stolons) creeping; rhizoids smooth, reddish brown, densely

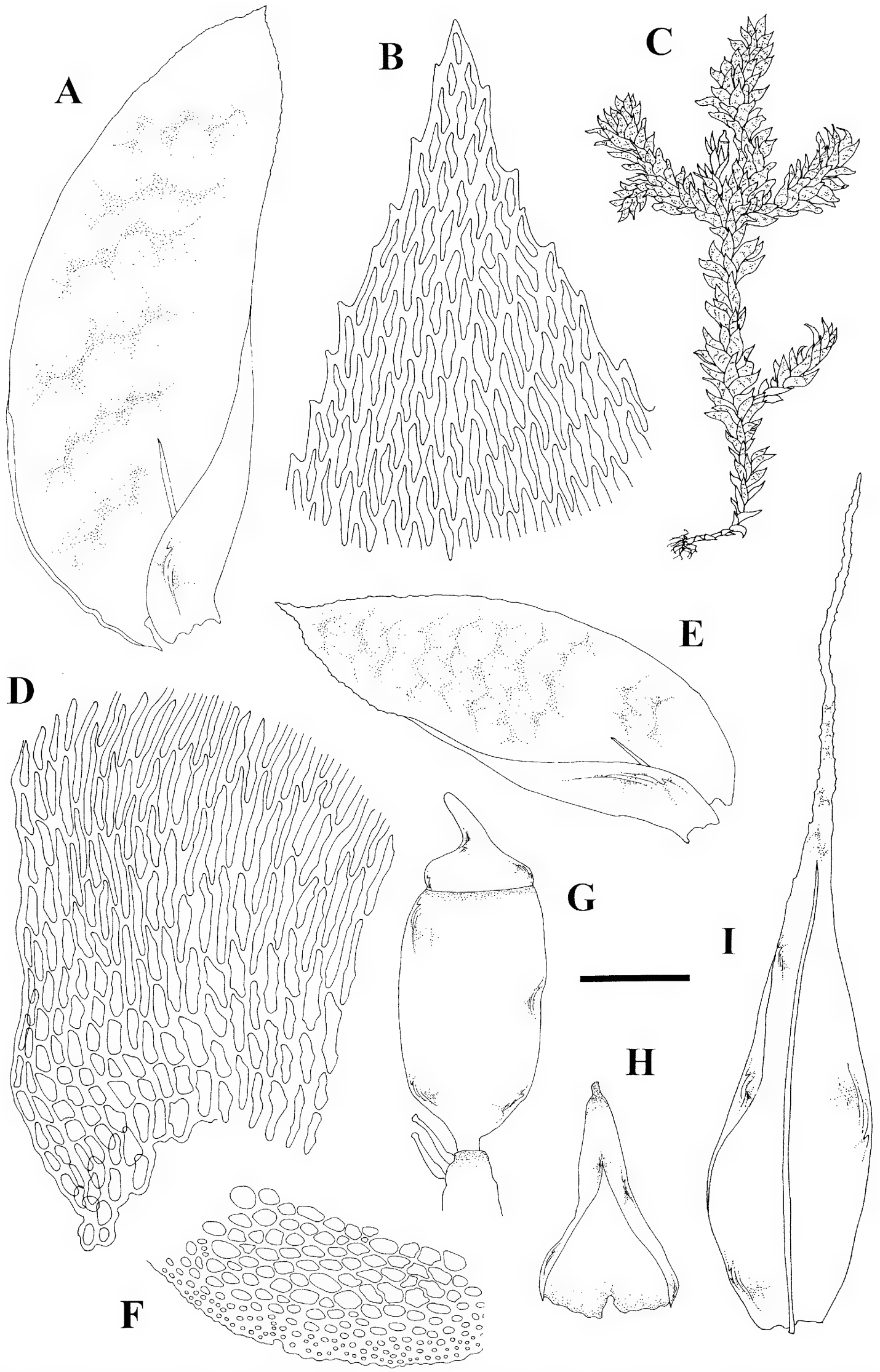
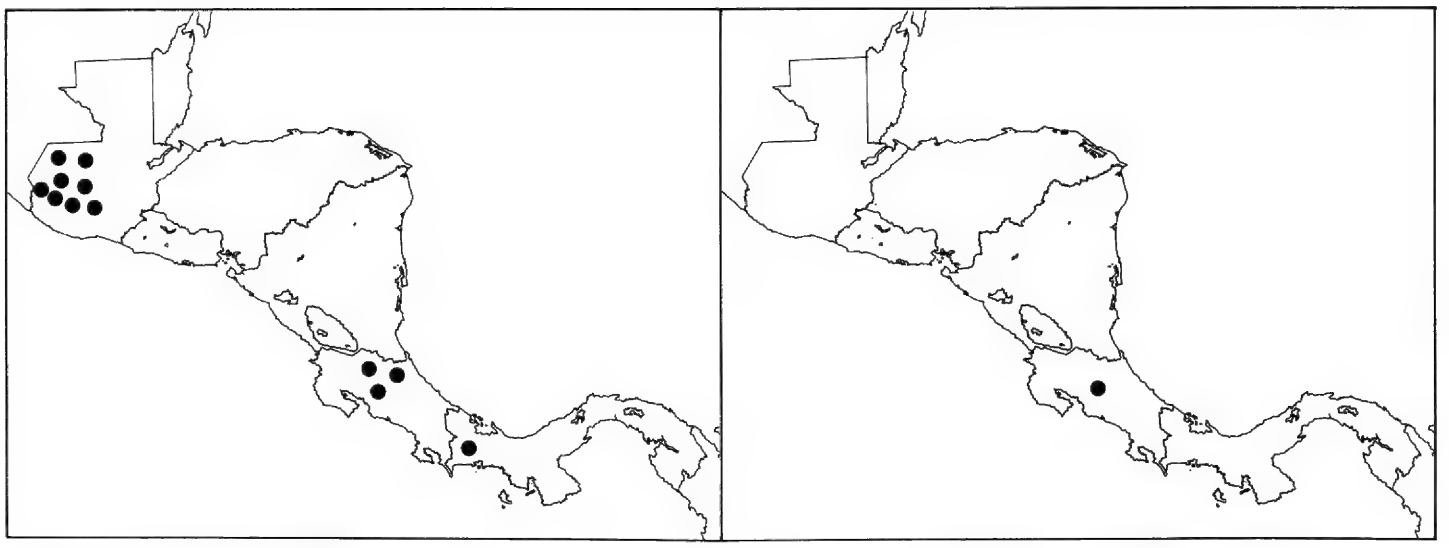


Figure 92. *Neckera ehrenbergii*. A & E. Leaves. B. Leaf apex. C. Habit. D. Basal and alar cells. F. Stem in cross section. G. Seta, capsule, and operculum. H. Calyptra. I. Perichaetial leaf. Scale in mm: bar = 0.06 (B, D); bar = 0.08 (F); bar = 0.6 (A, E, H); bar = 0.9 (G); bar = 1.0 (I); bar = 604 (C). C from *Davidse & D'Arcy 10183F*; A from *Richards 3957*; B, D, E from *Allen 9146*; all other figure parts from *Sharp 4964*.



Neckera ehrenbergii *Neckera scabridens*

present on stolons and on secondary stems and branches when in contact with substrate; leaves appressed to spreading, ovate-triangular, evenly foliate, 0.5–1.0 mm long. Secondary stems erect, horizontal or pendent, not stipitate, irregularly branched, complanate-foliate, at times flagellate-attenuate; secondary stems in cross section with sclerodermis of 3–5 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia abundant or sparse, uni- or multiseriate, often over 0.5 mm long; pseudoparaphyllia foliose. Secondary stem and branch leaves erect-spreading to spreading, undulate, oblong-ovate to oblong-lanceolate, 2.5–4.0 mm long, asymmetric, acute to broadly acute, decurrent, rounded to the insertion; margins subentire, serrulate or denticulate, broadly inflexed on one side below, narrowly recurved on other side to 1/4 the leaf length; costae faint, short and double, with one fork usually longer than the other; cells smooth, apical cells hexagonal, rhomboidal, or fusiform, 30–40 × 6–8 µm, firm- to thick-walled, at times porose; basal cells linear-fusiform, 60–80 × 4–8 µm, thick-walled, at times porose; alar cells weakly differentiated, 4–5 subquadrate cells at the extreme alar angle, cells across the insertions yellow. Autoicous. Perichaetial leaves oblong-subulate, subula smooth or undulate, 4–8 mm long; costae short and double to long and single. Setae very short, 0.12–0.25 mm, smooth, red. Capsules immersed, erect, cylindric, symmetric, 1.5–2.0 mm long; exothecial cells not strongly differentiated at mouth, those below rounded, subquadrate to short-rectangular, firm- or thick-walled; stomata absent; opercula conic-rostrate, 0.7–0.9 mm long; annuli rudimentary, of several layers of thin-walled, persistent cells; peristome diplolepideous; exostome teeth yellow to yellowish brown, narrowly triangular, 0.4–0.6 mm long, dorsal (outer) surface cross-striate at base, papillose to smooth above, trabeculae and median line faintly developed, ventral (inner) surface smooth to weakly papillose, trabeculae well developed; endostome light yellow, lightly papillose, basal membranes short, segments 0.2–0.6 mm long, broadly perforate, not keeled or thickened at the trabeculae, cilia rudimentary or absent. Spores 26–40 µm, densely papillose. Calyptrae cucullate, naked, smooth, 1.0–1.5 mm long.

Illustrations. Bartram (1949, Fig. 124 C–F); Sharp *et al.* (1994, Fig. 556). Figure 92.

Habitat. On bark of trees (*Abies*, *Alnus*, *Cupressus*, *Quercus*), often in cloud forests, occasionally on shaded or moist banks and on limestone; 1800–4000 m.

Distribution in Central America. GUATEMALA. Chimaltenango: *Richards et al. 2904* (F, MO); Huehuetenango: *Sharp 4964* (F, FH, MO, NY); Quetzaltenango: *Sharp 2122* (FH, MO, US); Quiché: *Richards 2957* (F, MO, NY); Sacatepéquez: *Standley 65246* (F, FH, US); San Marcos: *Standley 85419* (F, FH, NY, US); Sololá: *Steyermark 47240* (F, FH, NY); Totonicapán: *Standley 84422* (F, FH, NY). COSTA RICA. Alajuela: *Standley & Torres 47453a* (FH, US); Heredia: *Crosby* 9667 (MO); San José: *Polakowsky* (MO). PANAMA. Chiriquí: *Davidse & D'Arcy 10183F* (MO).

World range: Mexico; Central America.

Neckera ehrenbergii is a medium-sized moss restricted to high elevations in Central America. It has complanate-foliate stems and oblong-ovate to oblong-lanceolate leaves that are asymmetric as

well as distinctly undulate. The leaves are typically broadly acute and rounded to the insertion, with one broadly inflexed margin. The other margin is often narrowly recurved below. The capsules of *N. ehrenbergii* are immersed, lack stomata, and have peristomes with the exostome teeth horizontally striate at base and weakly developed endostomial segments.

There are two forms of *N. ehrenbergii* in Central America. In the type expression, the inner perichaetial leaves have very long, undulate subulae and often long, single costae. Its stems have abundant paraphyllia and its leaf margins are strongly recurved in the lower quarter of the leaf. Furthermore, the endostomial segments are weakly developed and have lamellae that are more or less rounded at the sides. The second expression is nomenclaturally centered on *Neckera chlorocaulis*. It has acuminate inner perichaetial leaves, with short double costae, stems with sparse (or even lacking) paraphyllia, and leaf margins that are mostly plane. Its endostomial segments are better developed than those of the *ehrenbergii*-expression and the lamellae are more or less straight sided. These two expressions have been treated at the species level by Bartram (1949) and Smith (1994). There are, however, many collections that exhibit a puzzling array of intermediate expressions of the above features. Sastre (1987) and Wagner (1951) treated the complex as a single species. Although a single species is provisionally recognized here, the problem is worthy of further study.

Neckera scabridens is the only other Central American species of *Neckera* with immersed capsules. It has sparse to absent stem paraphyllia, plane leaf margins, and acuminate inner perichaetial leaves that clearly separate it from the *ehrenbergii*-expression of *N. ehrenbergii*. The *chlorocaulis*-expression of *N. ehrenbergii*, however, has acuminate inner perichaetial leaves, leaf margins that are often plane, and variably developed (sometimes absent) stem paraphyllia. *Neckera scabridens* differs from the *chlorocaulis*-expression in having capsules with stomata and endostomial segments with nodose to appendiculate thickenings on the trabeculae.

3. *Neckera scabridens* Müll. Hal., Bot. Zeitung (Berlin) 5: 828. 1847. Protologue. Patria: Chile australis in truncis sylvarum umbrosarum ad Antuco Novbr., [collector not given]. Type (see Sastre 1987). BM, lectotype.

Neckera lindigii Hampe, Linnaea 32: 149. 1863. Protologue. [Colombia] Bogota Monserae, Tequendama, Canoas et Fusagasuga ad arbores, 1900–2900 metr., Jan.–Majo–Junio, [*Lindig*] *no. 2046*. Type (see Sastre 1987). Bogotá, *Lindig s.n.* (BM, lectotype).

Neckera bogotensis Mitt., J. Linn. Soc., Bot. 12: 454. 1869. Protologue. [Colombia] Andes Bogotenses, inter Tipaquira et Pacho (8000 ped.), ad arbores, *Weir*, *n. 275*. Type (see Sastre 1987). NY, holotype.

Plants medium-sized to large, 3–12 cm long, in usually flattened, pale green to yellowish green masses. Primary stems (stolons) creeping; rhizoids smooth, reddish brown, densely present on stolons and on secondary stems and branches when in contact with substrate; leaves erect, ovate-lanceolate, evenly foliate, 1–2 mm long. Secondary stems erect, horizontal or pendent, not stipitate, irregularly branched, complanate-foliate; secondary stems in cross section with sclerodermis of 3–5 rows of small, thick-walled cells, cortical cells enlarged, firm- to thick-walled, central strand absent; paraphyllia present or absent, uniseriate, less than 0.5 mm long; pseudoparaphyllia foliose. Secondary stem and branch leaves erect-spreading to spreading, undulate, oblong-ovate to oblong-lanceolate, 2.5–4.0 mm long, asymmetric, acute, decurrent, rounded to the insertion; margins subentire to serrulate, broadly inflexed on one side below, plane on other side; costae faint, short and double with one fork usually longer than the other; cells smooth, apical cells rhomboidal or fusiform, 24–50 × 6–8 µm, firm- to thick-walled, at times porose; basal cells linear-fusiform, 50–80 × 4–8 µm, thick-walled, often porose; alar cells weakly differentiated, 4–5 subquadrate cells at the extreme alar angle, cells across the insertions yellow. Autoicous. Perichaetial leaves oblong-lanceolate, 3–5 mm long; costae short and double or absent. Setae very short, 0.20 mm, smooth, red. Capsules immersed, erect, cylindric, symmetric, 1.5–2.0 mm long; exothecial cells not strongly differentiated at mouth, those below rounded, subquadrate to short-rectangular, firm- or thick-walled; stomata at capsule base; opercula conic-rostrate, 1.0–1.5 mm long; annuli rudimentary, of several layers of thin-walled, persistent cells; peristome diplolepideous; exostome teeth yellow to yellowish brown, narrowly triangular, 0.7–1.0 mm long, dorsal (outer) surface cross-striate at base, papillose to smooth above, trabeculae and median line faintly developed, ventral (inner) surface smooth to weakly papillose, trabeculae well developed;

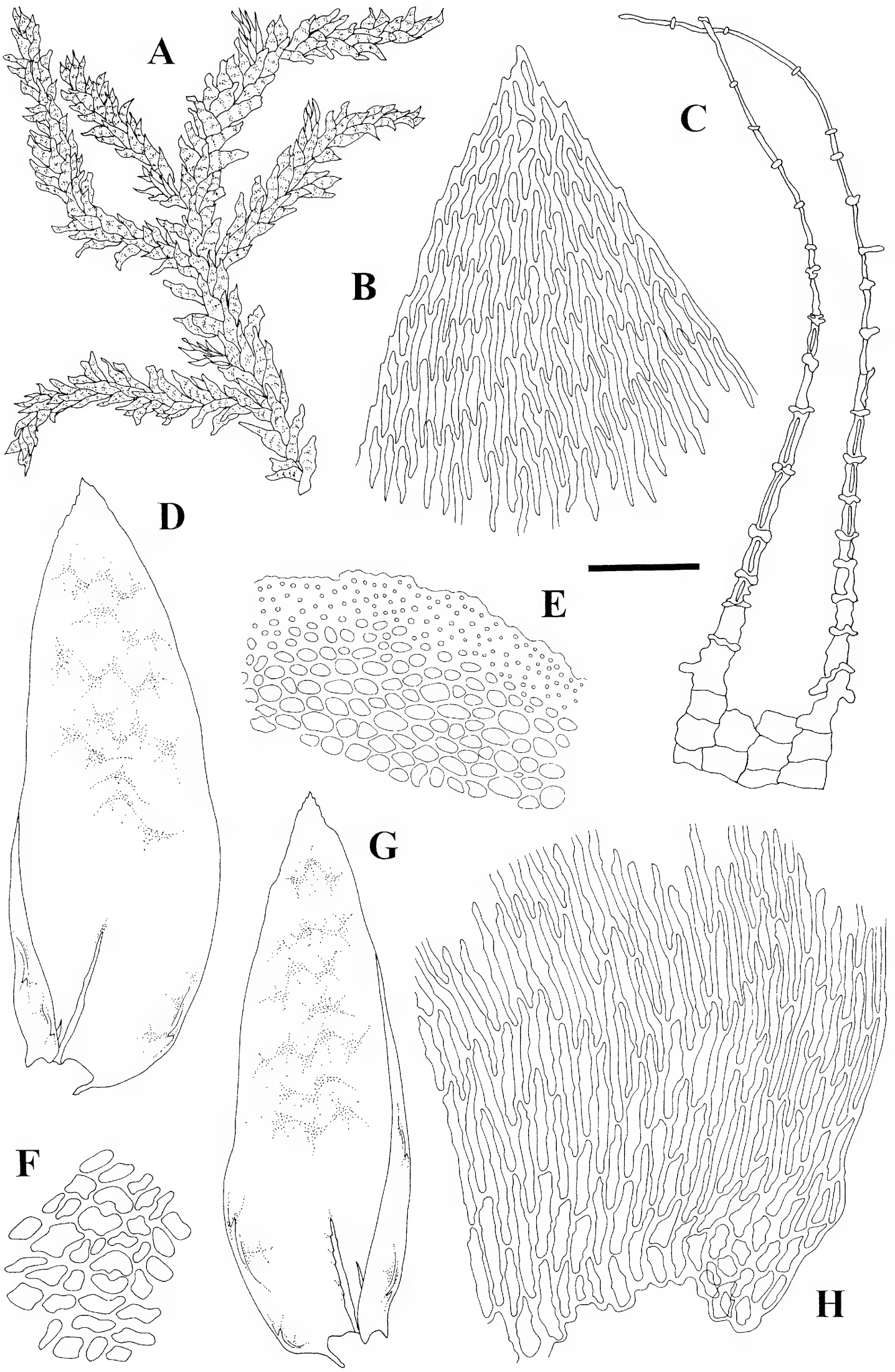


Figure 93. *Neckera scabridens*. A. Habit. B. Leaf apex. C. Endostome, ventral (inner) surface. D & G. Leaves. E. Stem in cross section. F. Stomata. H. Basal and alar cells. Scale in mm: bar = 0.06 (B, F, H); bar = 0.08 (E); bar = 0.1 (C); bar = 0.7 (D, G); bar = 8.0 (A). C from *Churchill 21421*; all other figure parts from *Crosby 6109*.

endostome light yellow, lightly papillose, basal membranes short, segments nearly as long as the exostome teeth, narrowly perforate, not keeled, cilia rudimentary or absent. Spores 26–32 µm, densely papillose. Calyptrae cucullate, naked, smooth, 1.0–1.5 mm long.

Illustrations. Buck (1998, Pl. 39 1–7); Gradstein *et al.* (2001, Fig. 159 F–J). Figure 93.
Habitat. Epiphytic; 2300–3130 m.
Distribution in Central America. COSTA RICA. San José: *Crosby & Crosby 6109* (MO).
World range: Mexico (Michoacán: *Verhoek-Williams et al. 607B*, MO); Central America; Caribbean; Western, Northern, and Southern South America, Brazil.

Neckera scabridens is a medium-sized moss of mostly South American distribution. In Central America it is known only from a few high elevation localities in Costa Rica. It has complanate-foliate stems and oblong-ovate to oblong-lanceolate leaves that are asymmetric and distinctly undulate. The leaves are typically broadly acute, rounded to the insertion, with margins broadly inflexed on one side and plane on the other. The capsules of *N. scabridens* are immersed and stomatose, with the peristomes having the exostome teeth horizontally striate at base.

Neckera ehrenbergii is the only other Central American species of *Neckera* with immersed capsules. It usually has abundant stem paraphyllia, leaf margins tightly recurved on one side, and setaceous inner perichaetial leaves. There is, however, a form of *N. ehrenbergii* (the *chlorocaulis*-expression) that has acuminate inner perichaetial leaves, leaf margins that are often plane, and variably developed (sometimes absent) stem paraphyllia. The *chlorocaulis*-expression of *N. ehrenbergii* differs from *N. scabridens* in having estomatose capsules and endostomial segments that lack nodose to appendiculate thickenings on the trabeculae.

The protologue of *N. scabridens* does not indicate the type collector. Furthermore, this information cannot be deduced from the paper, which lacks an introduction and lists species from a disparate group of collectors. In a later account of *N. scabridens* (Müller 1850), however, Müller cited the species with the exact same locality information but this time added "*Pöppig*" as the collector.

4. *Neckera urnigera* Müll. Hal., Syn. Musc. Frond. 2: 57. 1850. Protologue. Mexico. *Deppe et Schiede* pr. Xalapam legerunt. Types (see Sastre 1987). BM, lectotype; H, isolectotype.

Neckera microcarpa Schimp. *in* Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 221. 1872. Protologue. [Mexico] Mirador (*Liebmann* in herb. Par.). Type. Mexico. Mirador, *Leibmann* (MO, isotype).
Neckera wercklei Broth. & Thér., Recueil Publ. Soc. Havraise Études Diverses 88: 312. 1921. Protologue. [Costa Rica] La Palma, près San José, alt. 1500 m (*C. Werklé*, avril 1910). Type. Costa Rica. La Palma, près San José, alt. 1500 m. leg. *C. Werklé*, avril 1910 (FH, isotype), *syn. nov.*

Plants medium-sized to large, 3–10 cm long, in usually flattened, pale green to yellowish green masses. Primary stems (stolons) creeping; rhizoids smooth, reddish brown, densely present on stolons and on secondary stems and branches when in contact with substrate; leaves erect, evenly foliate, 1–1.7 mm long. Secondary stems erect, horizontal or pendent, not stipitate, irregularly branched, complanate-foliate; secondary stems in cross section with sclerodermis of 3–4 rows of small, thick-walled cells, cortical cells enlarged, firm- to thick-walled, central strand absent; paraphyllia present or absent, uniseriate, less than 0.5 mm long; pseudoparaphyllia foliose. Secondary stem and branch leaves spreading, occasionally erect-spreading, undulate, oblong-lanceolate, 2.5–4.0 mm long, asymmetric, acute; margins subentire to serrulate, broadly inflexed on one side below, plane or narrowly recurved on other side, non-inflexed side long-decurrent and straight to the insertion; costae faint, short and double with one fork usually longer than the other; cells smooth, apical cells rhomboidal or long fusiform, 24–50 × 6–8 µm, firm- to thick-walled; basal cells linear-fusiform, 50–80 × 4–8 µm, thick-walled, often porose; alar cells not or very weakly differentiated, 1–3 subrectangular cells at the extreme alar angle, cells across the insertions yellow. Autoicous. Perichaetial leaves oblong-lanceolate, 2–3 mm long; costae short and double or absent. Setae 2.0–2.5 mm, smooth, yellow red. Capsules exserted, erect, cylindric, symmetric, 1.0–1.5 mm long; exothecial cells not strongly differentiated at mouth, those below short-rectangular, firm- or thick-walled; stomata on capsule base; opercula conic-rostrate, 0.5 mm long; annuli rudimentary, of several layers of thin-walled, persistent cells; peristome

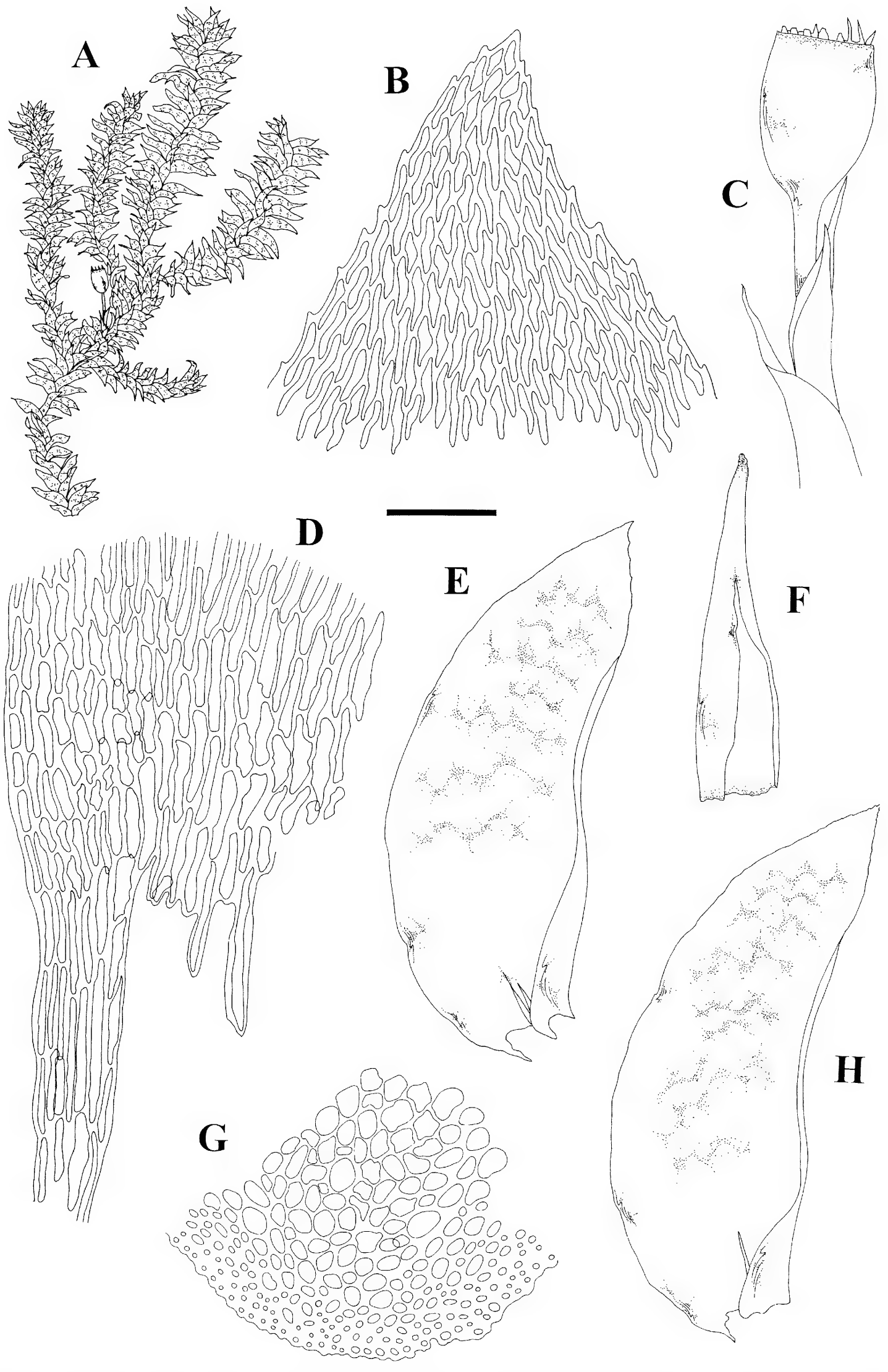
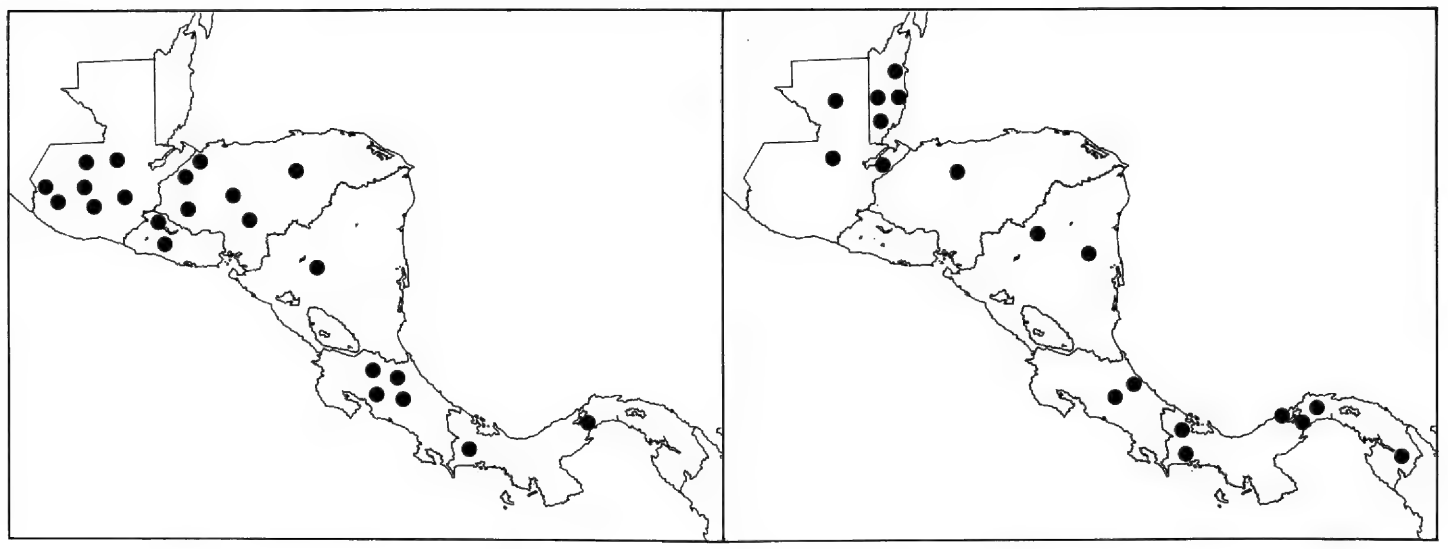


Figure 94. *Neckera urnigera*. A. Habit. B. Leaf apex. C. Seta and capsule. D. Basal and alar cells. E & H. Leaves. F. Calyptra. G. Stem in cross section. Scale in mm: bar = 0.06 (B, D); bar = 0.08 (G); bar = 0.6 (E, F, H); bar = 0.9 (C); bar = 6.4 (A). All figure parts from *Allen 12860*.



Neckera urnigera *Neckeropsis disticha*

diplolepideous; exostome teeth whitish yellow, narrowly triangular, 0.4–0.5 mm long, dorsal (outer) surface cross-striate at base, papillose to smooth above, trabeculae and median line faintly developed, ventral (inner) surface smooth to weakly papillose, trabeculae well developed; endostome light yellow, lightly papillose, basal membranes short, segments nearly as long as the exostome teeth, perforate, not keeled, more strongly thickened on the ventral (inner) surface than on the dorsal (outer) surface, cilia rudimentary or absent. Spores 18–30 µm, densely papillose. Calyptrae cucullate, naked, smooth, 2.0 mm long.

Illustrations. Thériot (1921, Fig. 6); Bartram (1949, Fig. 125 A–C); Sharp *et al.* (1994, Fig. 554); Buck (1998, Pl. 39 8–18). Figure 94.

Habitat. On tree and treelet trunks, branches, and twigs; 1400–3048 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: *Standley 70010b* (F, FH); Chimaltenango: *Standley* 62030a (F, FH, MO); Jalapa: *Clover 10199* (FH, MO); Quetzaltenango: *Standley 85511* (F, FH); Quiché: *Sharp 2424* (FH, US); Sacatepéquez: *Standley 63711* (F, FH); San Marcos: *Sharp 5499* (MO). EL SALVADOR. Chalatenango: *Sipman 37800* (NY); San Salvador: *Munro et al. 2242* (BM, MO). HONDURAS. Comayagua: *Olson 84-31b* (MO); Cortés: *Allen 14150* (MO); Francisco Morazán: *Richards et al. 3543a* (F); Lempira: *Allen 11118* (MO); Olancho: *Allen 12860* (MO); Santa Bárbara: *Allen 11808* (MO). NICARAGUA. Matagalpa: *Richards et al. 3756* (F). COSTA RICA. Alajuela: *Crosby & Crosby 6289* (MO); Cartago: *Dodge 3982* (FH); Heredia: *Gómez 20056* (CR, MO, NY, US); San José: *Crosby & Crosby 8568* (MO). PANAMA. Canal Area: *Dodge 3982a* (MO); Chiriquí: *Nee 9925a* (MO).

World range: Mexico; Central America; Caribbean; Western, Northern, and Southern South America, Brazil.

Neckera urnigera is a medium-sized to large moss found at mostly high elevations in Central and South America. In the Caribbean it occurs only on Hispaniola. It has complanate-foliate stems with paraphyllia present or absent, and oblong-lanceolate leaves that are asymmetric, distinctly undulate, and nearly always spreading when dry. The leaves are typically broadly acute, with margins broadly inflexed on one side and either narrowly recurved or plane on the other side. On the non-inflexed side, the leaves are straight to the insertions and long-decurrent. The alar cells on the non-inflexed side of the leaves are nearly undifferentiated, while those on the other side consist of 3–5 subrectangular, hyaline to light reddish cells. *Neckera urnigera* has exserted, stomatose capsules and peristomes, with the exostome teeth horizontally striate at base.

Neckera chilensis is the only other Central American species of *Neckera* with exserted capsules. The two species are very similar, but the leaves of *N. chilensis* differ from those of *N. urnigera* in being mostly erect-spreading rather than spreading. The leaves of the two species also differ in their alar regions. In *N. chilensis* the leaves on the non-inflexed side are subauriculate or rounded to the insertions, shortly decurrent, and the alar cells consist of 6–10 subquadrate, reddish yellow cells. Fur-

thermore, the sporophytes of *N. chilensis* are somewhat larger than those of *N. urnigera*, with setae often 3 mm long and capsules nearly 2 mm long.

Neckera microcarpa was treated as a synonym of *N. ehrenbergii* by Wagner (1951), but Sastre (1987) and Smith (1994) considered it a synonym of *N. urnigera*. The type specimen in MO is gametophytically the same as *N. urnigera*. The MO specimen lacks sporophytes, but Bescherelle (1872) included it in the *Neckera* group with exserted capsules.

5. *Neckeropsis* Reichardt, Verh. Zool.-Bot. Ges. Wien 18(Abh.): 192. 1868.

Paraphysanthus Spruce, Cat. Musc. 19. 1867, invalid name, lacks a description. *Neckera* Hedw. sect. *Himantocladium* Mitt. subsect. *Paraphysanthus* Mitt., J. Linn. Soc., Bot. 12: 450. 1869. *Neckera* sect. *Paraphysanthus* (Mitt.) Broth., Nat. Pflanzenfam. I(3): 840. 1906. *Neckeropsis* sect. *Paraphysanthus* (Mitt.) M. Fleisch., Musci Buitenzorg 3: 876. 1908.

Neckera Hedw. sect. *Taeniocladium* Mitt., J. Linn. Soc., Bot. 10: 168. 1868. *Neckera* sect. *Himantocladium* Mitt. subsect. *Taeniocladium* (Mitt.) Mitt., J. Linn. Soc., Bot. 12: 450. 1869. *Neckeropsis* sect. *Taeniocladium* (Mitt.) M. Fleisch., Musci Buitenzorg 3: 879. 1908.

Plants small, medium-sized, or large, yellowish to green or light green, dull, at times with an intense blackish color. Primary stems (stolons) creeping; rhizoids smooth, reddish brown, densely present on stolons and on secondary stems and branches when in contact with substrate; leaves appressed to spreading, scarious. Secondary stems pendent, ascending or erect, variously stipitate, simple to irregularly pinnate, complanate-foliate, at times flagellate-attenuate; secondary stems in cross section with sclerodermis, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia foliose to subfilamentous. Stipe leaves evenly foliate, erect to erect-spreading. Secondary stems and branches complanate-foliate; leaves wide-spreading, strongly undulate, smooth or crisped when dry, strongly undulate or flat when wet, broadly oblong to oblong-ligulate, asymmetric, broadly rounded-obtuse to truncate, retuse or broadly apiculate, narrowly or not decurrent, rounded or auriculate at base; margins crenulate-serrulate at apex, distantly serrulate below, inflexed on one side below; costae single, extending 1/2–3/4 the leaf length, often forked or branched near tip (outside the region sometimes short and double or nearly absent); cells smooth, apical cells hexagonal to rhombic, at times horizontally rectangular in 1–3 rows, median cells rhomboidal, linear-fusiform near insertion, marginal cells on inflexed side of leaf elongate-linear, at times forming a more or less distinct border; alar cells weakly differentiated, cells across the insertions porose. Asexual propagula absent in Central America, deciduous microphyllous branches outside the region. Synoicous or autoicous. Perichaetia at times ramentose, ramenta loriform to linear. Sporophyte at times elevated at maturity by a pseudopodium. Setae short. Capsules immersed, emergent to short-exserted, erect, symmetric, broad-cylindric; exothecial cells oblate at mouth, short-rectangular below; stomata absent; opercula short, obliquely rostrate; annuli rudimentary; peristome diplolepideous, inserted within the capsule mouth; exostome teeth pale yellow, linear, papillose, trabeculae and median line weakly developed; endostome yellow, papillose, basal membranes short, segments linear, weakly and narrowly perforate, not keeled, cilia absent. Spores irregularly rounded, lightly papillose. Calyptrae cucullate or mitrate and lobed, smooth or densely ramentose.

Neckeropsis is a genus of 30 species (Crosby *et al.* 2000) found primarily in the tropical regions of the world. The Asiatic species of *Neckeropsis* were revised by Touw (1962), the Neotropical species by Sastre (1987), and the African species by Enroth (1993). Further refinements to the taxonomy of *Neckeropsis* were made by Enroth (1989, 1995), Enroth and Magill (1994), Ochyra and Enroth (1989), Touw (1972), and Touw and Ochyra (1987).

Plants of *Neckeropsis* frequently have an intense black coloration that is more often associated with the Meteoriaceae. Although the genus is not considered to have stipitate stems, plants of *Neckeropsis* are incredibly variable in this respect, and single collections can sometimes have plants with both stipitate and nonstipitate stems. In this respect *Neckeropsis* closely resembles *Orthostichella*. *Neckeropsis* has strongly flattened leaves that appear to be arranged in four rows, but they are actually in eight rows (Wijk 1957; Touw 1962). This condition is termed pseudotetrastichous

(Wijk 1957). The leaves are often strongly undulate, truncate or broadly rounded at the apex, and often auriculate at base. The Central American species of *Neckeropsis* have long single costae that are often spurred or forked above, but species outside the region sometimes have very short, faint costae. The leaf cells are smooth, generally rhomboidal to oblong-rectangular, and the alar cells are poorly differentiated. An especially odd feature of some of the species is the presence of numerous ramenta that develop in perichaetia after fertilization. This feature also appears correlated with considerable post-fertilization elongation of the vaginulae, which can be interpreted as a pseudopodium (Touw 1962). The setae in *Neckeropsis* are short and the capsules are often immersed. The calyptrae can be either cucullate or mitrate and naked or hairy.

In Central America *Neckeropsis* is most easily confused with *Neckera*, since both genera have the same aspect and plants with strongly undulate leaves. Central American species of *Neckera* differ from *Neckeropsis* in having acute leaves with short, double costae and sometimes exserted capsules. The Central American species of *Neckera* with immersed capsules also have abundant paraphyllia, and this feature is lacking in *Neckeropsis*. Touw (1962) and Enroth (1989) considered *Neckeropsis* most closely related to the Malayan–West Pacific genus *Himantocladium* (Mitt.) M. Fleisch. Touw (1962) considered *Himantocladium* to differ from *Neckeropsis* in having short-stalked capsules; more clearly 8-ranked leaves that were irregularly undulate, often strongly and coarsely serrate at the apex; rounded, non-auriculate leaf bases often widened at base; and irregularly arranged leaf cells with very thick walls. Enroth (1992) further distinguished *Himantocladium* from *Neckeropsis* in having exserted, stomatose capsules. Both authors noted a number of intermediate or transitional species, and Enroth (1992) considered the presence of stomata to be the only "unequivocal generic distinction" between the genera.

The name *Neckeropsis* combines the generic name *Neckera* with the Greek noun *opsis* (aspect, appearance).

1. Leaves smooth to crispate when dry, flat when wet; leaf base not auriculate; calyptra cucullate . . . . . 1. *N. disticha*
1. Leaves strongly undulate when wet or dry; leaf base auriculate; calyptra mitrate 2
2. Perichaetial leaves oblong-subulate, 3–4 mm long; ramenta absent . . . . . 2. *N. foveolata*
2. Perichaetial leaves ovate-subulate, 1 mm long; ramenta present . . . . . 3. *N. undulata*

1. *Neckeropsis disticha* (Hedw.) Kindb., Canad. Rec. Sci. 6: 21. 1894. *Neckera disticha* Hedw., Sp. Musc. Frond. 201. 1801. *Fontinalis disticha* Sw., Prodr. 138. 1788, illegitimate name. *Pilotrichum distichum* (Hedw.) P. Beauv., Prodr. Aethéogam. 83. 1805. *Daltonia disticha* (Hedw.) Arn., Mém. Soc. Linn. Paris 5: 295. 1826. *Neckera retusa* Brid., Bryol. Univ. 2: 243. 1827, illegitimate new name, includes an earlier name in synonymy. *Distichia retusa* (Brid.) Brid., Bryol. Univ. 2: 787. 1827, illegitimate name. *Eleutera disticha* (Hedw.) Stuntz, Bull. Torrey Bot. Club 27: 209. 1900. *Rhystophyllum distichum* (Hedw.) E. Britton, Bryologist 8: 6. 1904. Protologue. Habitat in Jamaica; in arborum truncis, ut Dillenio videbatur.

Plants small to large, 3–7 cm long, yellowish to green or light green, dull. Primary stems (stolons) creeping; rhizoids smooth, reddish brown, densely present on stolons and on secondary stems and branches when in contact with substrate; leaves appressed to spreading, scarious. Secondary stems pendent, ascending or erect, variously stipitate, simple to irregularly pinnate, complanate-foliate, at times flagellate-attenuate; secondary stems in cross section with sclerodermis of 3–5 rows of small, thick-walled cells, cortical cells enlarged, somewhat thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia narrowly foliose to subfilamentous, lanceolate, serrulate on margins. Stipe leaves evenly foliate, erect to erect-spreading. Secondary stems and branches complanate-foliate; leaves wide-spreading, smooth to crisped when dry, flat when wet, broadly oblong, 1.0–1.7 mm long, asymmetric, broadly rounded-obtuse to truncate, retuse to broadly apiculate, narrowly decurrent, rounded, not auriculate at base; margins crenulate-serrulate at apex, distantly serrulate below, inflexed on one side below; costae single, extending 1/2–3/4 the leaf length, often forked or branched near tips; cells smooth, apical cells hexagonal to rhombic, to 8 µm long, median cells rhomboidal, 16–18 µm

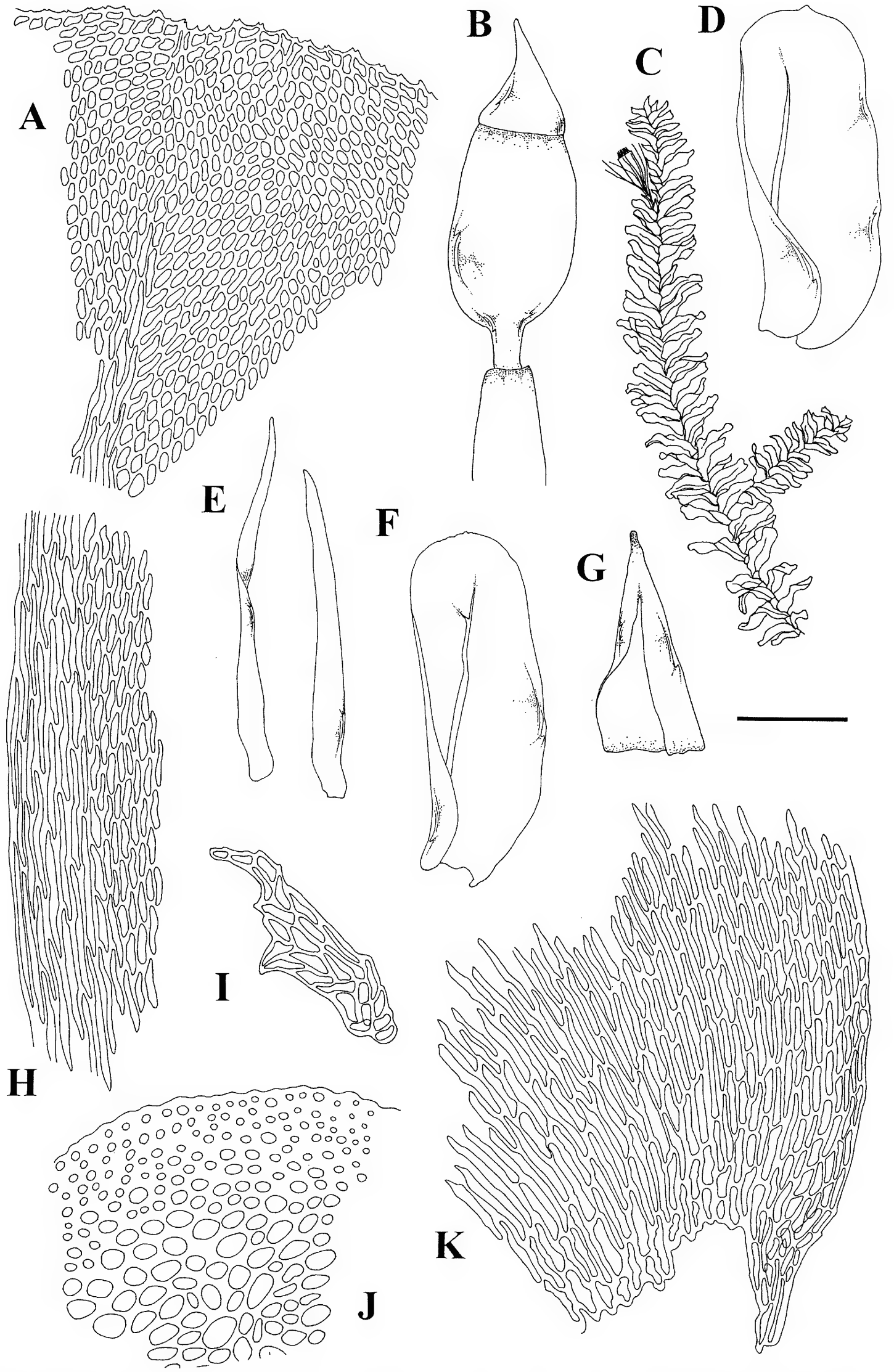


Figure 95. *Neckeropsis disticha*. A. Leaf apex. B. Seta, capsule, and operculum. C. Habit. D & F. Leaves. E. Paraphyses. G. Calyptra. H. Median leaf cells and margin. I. Pseudoparaphyllia. J. Stem in cross section. K. Basal and alar cells. Scale in mm: bar = 0.06 (A, H–K); bar = 0.5 (G); bar = 0.6 (D–F); bar = 0.7 (B); bar = 3.2 (C). H, K from *Johnson 3416*; all other figure parts from *Allen 18329*.

long, linear-fusiform near insertion, marginal cells on inflexed side of leaf elongate-linear, at times forming a more or less distinct border, thick- to firm-walled, not porose; alar cells weakly differentiated, of 2–5 short-rectangular cells at the basal angles, cells across the insertions porose. Asexual propagula absent. Synoicous. Perichaetia ramentose, ramenta loriform to linear, 1.7–2.0 mm long; perichaetial leaves ovate to oblong-ovate. Sporophyte elevated at maturity by a pseudopodium. Setae red, smooth, 0.2–0.5 mm long. Capsules immersed, emergent to short-exserted, erect, symmetric, broad-cylindric, 1.0–1.5 mm long; exothecial cells oblate at mouth in 5–7 rows, those below short-rectangular, firm-walled; stomata absent; opercula short, obliquely rostrate, 0.5 mm long; annuli rudimentary, of small, thin-walled cells; peristome diplolepideous, inserted within the capsule mouth; exostome teeth pale yellow, linear, to 300 µm long, papillose throughout on both sides, trabeculae and median line weakly developed; endostome yellow, papillose throughout, basal membranes short, barely exceeding the capsule mouth, segments linear to 1300 µm long, weakly and narrowly perforate, not keeled, cilia absent. Spores irregularly rounded, 12–15 µm, lightly papillose. Calyptrae cucullate, naked, to 1 mm long.

Illustrations. Bartram (1949, Fig. 125 G–H); Breen (1963, Pl. 105 1–5); Florschütz (1964, Fig. 106); De Sloover (1977, Figs. 72–91); Crum and Anderson (1981, Fig. 387); Florschütz-de Waard (1986, Fig. 106); Sharp *et al.* (1994, Fig. 553); Duarte Bello (1997, Pl. 212); Buck (1998, Pl. 40 9–16); Buck (2003, Fig. 106 I–P). Figure 95.

Habitat. On tree trunks, buttress roots, roots, branches, vines, twigs, often along streams and rivers, on rocks in streams, and on moist soil or mud banks; sea level to 900 m.

Distribution in Central America. BELIZE. Belize: *Lundell 2002* (FH); Cayo: *Allen 18326* (BRH, MO); Stann Creek: *Mains 2144* (FH); Toledo: *Whittemore 6313* (BRH, MO). GUATEMALA. Alta Verapaz: *Steyermark* 45039 (F, FH, MO, NY); Izabal: *Standley 24449a* (FH, MO, NY, US); Petén: *Bartlett 12452* (FH, US). HONDURAS. Yoro: *Allen* 13528 (MO). NICARAGUA. Jinotega: *Stevens* 16575 (HNMN, MO); Zelaya: *Proctor 27053* (MO, NY). COSTA RICA. Cartago: *Crosby 3654* (MO); Limón: *Daly 49* (MO). PANAMA. Bocas del Toro: *Lewis et al. 899* (MO, PMA); Canal Area: *Steyermark & Allen 17260* (FH, MO, NY); Chiriquí: *Cornman 3036* (F, MO); Colón: *Hammel 2690* (MO); Darién: *Allen 8817* (MO); Panamá: *Pittier 2350* (NY, US).

World range: Southeastern U.S.A.; Mexico; Central America; Caribbean; Western, Northern, and Southern South America, Brazil; West, West-Central, and East Tropical Africa, Western Indian Ocean.

Neckeropsis disticha is often a small plant; however, the species is extremely variable in size, and plants growing in or around streams at times become robust. Its plants are often distinctly stipitate, and have strongly complanate-foliate secondary stems and branches. Stipitate stems, however, are not a consistent feature of the species. The oblong leaves of *N. disticha* are usually widely spaced and crispate when dry. They have long, single costae that are often forked above and broadly rounded to truncate, crenulate-serrulate apices. The leaf cells are hexagonal to rhombic above, elongate below, and long-linear in several rows along the margins on the inflexed side of the leaf. The capsules are emergent to short-exserted, and the perichaetia are densely ramentose.

Neckeropsis undulata and *N. foveolata* differ from *N. disticha* in having auriculate leaves that are strongly undulate whether wet or dry. Both species further differ from *N. disticha* in having longer apical leaf cells, and *N. foveolata* also differs in lacking perichaetial ramenta. The naked calyptrae of *N. disticha* have been used to distinguish it from *N. undulata*, which has a hairy calyptra (Florschütz 1964); however, Sastre (1987) and Buck (1998) report the calyptrae of *N. undulata* to vary from naked to hairy. Nevertheless, the two species do differ in calyptra shape: *N. undulata*, mitrate; *N. disticha*, cucullate. Although the use by Churchill and Linares (1995) of leaf length/width differences (*N. disticha*: 1–1.4/0.7; *N. undulata*: 1.5–2.2/1.0) will often separate the two species, there is too much size variation in both species for this feature to consistently distinguish them. Buck (1998, 2003) found Caribbean collections of *N. undulata* to differ from *N. disticha* in having capsules that were immersed, with the ramenta overtopping the capsules. In Central America the capsules of *N. disticha* vary from immersed to emergent or short-exserted.

2. *Neckeropsis foveolata* (Mitt.) Broth., Nat. Pflanzenfam. (ed. 2) 11: 188. 1925. *Neckera foveolata* Mitt., Trans. Linn. Soc. London 23: 53. 1860. Protologue. Afrique (Beauvois in Hb. Hooker).

Plants medium-sized to large, to 16 cm long, dull, yellowish to green or light green, at times with an intense blackish color. Primary stems creeping; rhizoids smooth, reddish brown, densely present on stolons and on secondary stems and branches when in contact with substrate; leaves spreading, evenly foliate, 0.8–1.2 mm long, ligulate, clasping at base. Secondary stems pendent, ascending or erect, variously stipitate, simple to irregularly pinnate, complanate-foliate, at times flagellate-attenuate; cross section of secondary stems with sclerodermis of 3–5 rows of small, thick-walled cells, cortical cells enlarged, somewhat thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia narrowly foliose to subfilamentous, lanceolate, serrulate on margins. Stipe leaves evenly foliate, erect to erect-spreading. Secondary stems and branches complanate-foliate; leaves wide-spreading, strongly undulate when wet or dry, oblong-ligulate, 1.8–2.5 mm long, asymmetric, broadly rounded to truncate, not decurrent, clasping at base, rounded, cordate to auriculate at base; margins crenulate-serrulate at apex, distantly serrulate below, inflexed on one or both sides below; costae single, extending 1/2–3/4 the leaf length, occasionally forked; cells smooth, apical marginal cells horizontally rectangular in 1–3 rows, 8–16 µm long, subapical cells irregularly rectangular to rhombic, 10–20 µm long, median cells irregularly rhomboidal, 12–30 µm long, linear-fusiform toward insertion; alar cells weakly differentiated, of 2–5 short-rectangular cells at the basal angles, cells across the insertions yellowish, porose. Asexual propagula absent. Autoicous. Perichaetia without ramenta; perichaetial leaves oblong-subulate, 3.5–4.0 mm long. Setae red, smooth, 0.2–0.5 mm long. Capsules immersed, erect, symmetric, broad-cylindric, 1.4–1.5 mm long; exothecial cells oblate at mouth in 5–7 rows, those below rectangular, firm-walled; stomata absent; opercula obliquely rostrate, 0.5–1.0 mm long; annuli rudimentary, of small, thin-walled cells; peristome diplolepideous, inserted within the capsule mouth; exostome teeth pale yellow to whitish, linear, to 500 µm long, papillose throughout on both sides, trabeculae and median line weakly developed; endostome yellow, papillose throughout, basal membranes short, barely exceeding the capsule mouths, segments linear, to 500 µm long, weakly and narrowly perforate, not keeled, cilia absent. Spores irregularly rounded, 12–18 µm, lightly papillose. Calyptrae mitrate, lobed, smooth, to 1 mm long.

Illustrations. Dusén (1895, Figs. a–f, p. 35; Pl. 1, 5; Pl. 3, 4, as *Distichia afro-victoriae*); Bartram (1949, Fig. 126 A–B). Figure 96.

Habitat. On tree trunks, twigs, and shrubs; 300–700 m.

Distribution in Central America. BELIZE. Cayo: *Allen 18302* (MO); Toledo: *Whittemore 6468* (BRH, MO, NY). GUATEMALA. Izabal: *Steyermark 41879a* (F, FH). HONDURAS. Atlántida: *Allen 17467A* (MO). COSTA RICA. Alajuela: *Brenes 17029* (FH, MO, NY); Puntarenas: *Crosby 2688* (MO). PANAMA. Chiriquí: *Croat 33089C* (MO); Veraguas: *Crosby 10254* (MO).

World range: Central America; Northern South America, Brazil; West and West-Central Tropical Africa.

Neckeropsis foveolata has leaves that are strongly undulate whether wet or dry, usually truncate, and cordate to auriculate at base. Sporophytically, the species is distinguished by its lack of perichaetial ramenta, elongate perichaetial leaves, and immersed capsules. Although *Neckeropsis foveolata* is widespread in Africa, it appears to be an uncommon species in Central America. As noted by Sastre (1987), it differs from *N. undulata* (the most common Central American species of *Neckeropsis*) only in lacking perichaetial ramenta and in having longer (3.5–4.5 mm vs. 1.5–2.8 mm) perichaetial leaves that consistently overtop the operculate capsules. As a result, sterile collections of these two species cannot be distinguished from one another. Furthermore, in Central America *N. foveolata* sometimes grows mixed with *N. undulata*, but mixed collections in which only one species has sporophytes cannot be recognized as such. It is therefore possible that *N. foveolata* is more common in Central America than is presently indicated by herbarium collections. Plants of *N. foveolata* are sometimes tinged with an intense blackish color. This feature is often encountered in the Meteoriaceae and may be indicative of a close relationship between the two families.

Neckeropsis disticha differs from *N. foveolata* in having non-auriculate leaves that are smooth to crisped when dry and flat when wet. Furthermore, the apical leaf cells of *N. disticha* are shorter than

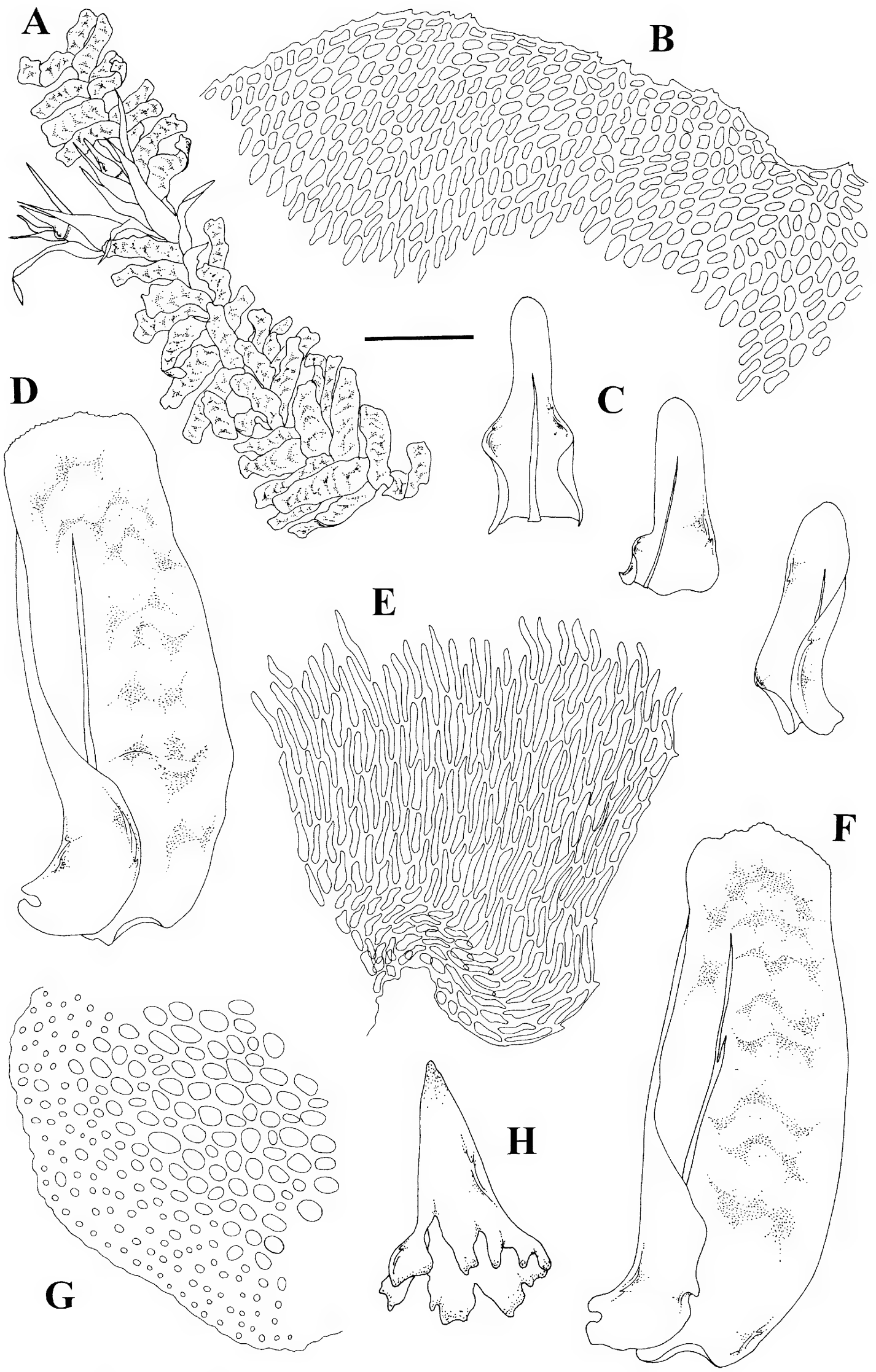
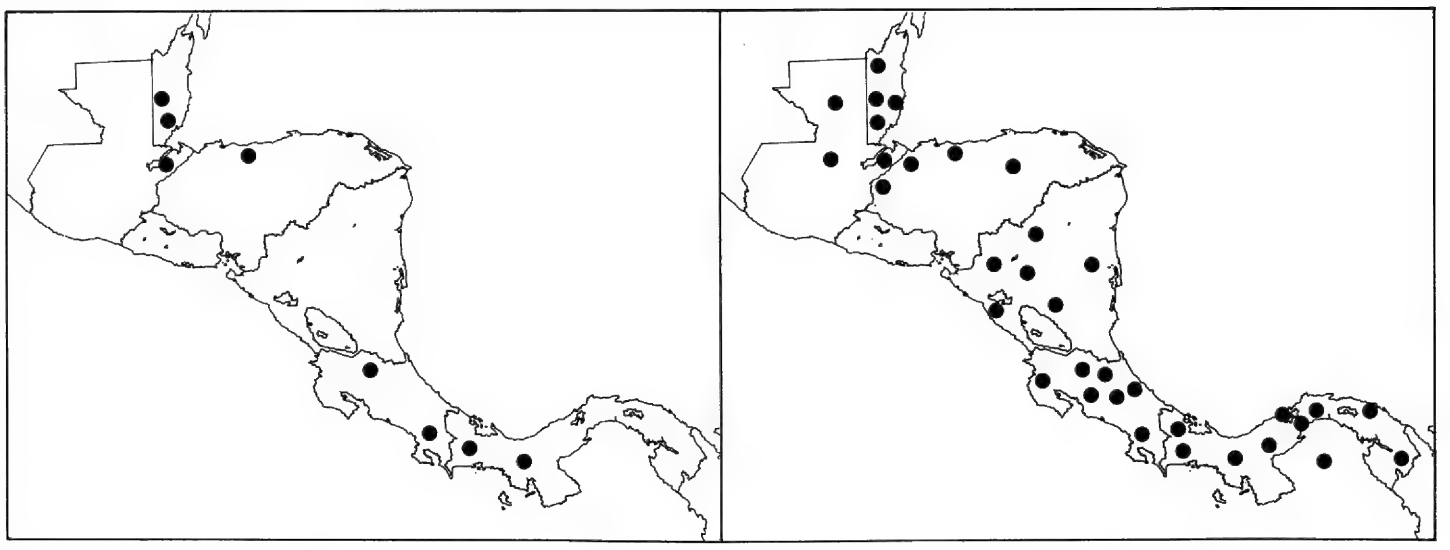


Figure 96. *Neckeropsis foveolata*. A. Habit. B. Leaf apex. C. Stolon leaves. D & F. Leaves. E. Basal and alar cells. G. Stem in cross section. H. Calyptra. Scale in mm: bar = 0.06 (B, E, G); bar = 0.4 (H); bar = 0.5 (C, D, F); bar = 2.0 (A). All figure parts from *Allen 18302*.



Neckeropsis foveolata *Neckeropsis undulata*

those of *N. foveolata*, and it has numerous perichaetial ramenta. The two species also differ in calyptra shape: *N. foveolata*, mitrate; *N. disticha*, cucullate.

3. *Neckeropsis undulata* (Hedw.) Reichardt, Verh. Zool.-Bot. Ges. Wien 18(Abh.): 192. 1868. *Neckera undulata* Hedw., Sp. Musc. Frond. 201. 1801. *Pilotrichum undulatum* (Hedw.) P. Beauv., Prodr. Aethéogam. 83. 1805. *Daltonia undulata* (Hedw.) Arn., Mém. Soc. Linn. Paris 5: 295. 1826. *Distichia undulata* (Hedw.) Brid., Bryol. Univ. 2: 787. 1827. Protologue. Habitat in Jamaica; in arborum truncis, ut Dillenio videbatur.

Plants medium-sized to large, to 7 cm long, dull, yellowish to green or light green, at times with an intense blackish tinge. Primary stems (stolons) creeping; rhizoids smooth, reddish brown, densely present on stolons and on secondary stems and branches when in contact with substrate; leaves spreading, evenly foliate, 0.8–1.2 mm long, ligulate, clasping at base. Secondary stems pendent, ascending or erect, variously stipitate, simple to irregularly pinnate, complanate-foliate; secondary stems in cross section with sclerodermis of 3–5 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia broadly foliose. Stipe leaves evenly foliate, erect to erect-spreading. Secondary stems and branches complanate-foliate; leaves wide-spreading, strongly undulate when wet or dry, oblong-ligulate, 1.4–2.5 mm long, asymmetric, broadly rounded to truncate, not decurrent, clasping at base, rounded, cordate to auriculate at base; margins crenulate-serrulate at apex, distantly serrulate below, inflexed on one or both sides below; costae single, extending 1/2–3/4 the leaf length, occasionally forked; cells smooth, apical cells horizontally rectangular, irregularly rectangular to rhombic, 8–18 µm long, median cells irregularly rhomboidal, 15–30 µm long, linear-fusiform toward insertion; alar cells weakly differentiated, of 2–5 short-rectangular cells at the basal angles, cells across the insertions yellowish, porose. Asexual propagula absent. Autoicous and synoicous. Perichaetia with ramenta; perichaetial leaves oblong-subulate to loriform, 1.5–3.0 mm long. Sporophyte elevated at maturity by a pseudopodium. Setae red, smooth, 0.2–0.3 mm long. Capsules immersed, erect, symmetric, cylindric to broad-cylindric, 1.4–1.8 mm long; exothecial cells quadrate to rounded at mouth in 5–6 rows, those below rectangular, firm-walled; stomata absent; opercula obliquely rostrate, 1.0 mm long; annuli rudimentary, of small, thin-walled cells; peristome diplolepideous, inserted within the capsule mouth; exostome teeth pale yellow, linear, to 500 µm long, lightly papillose throughout on both sides, trabeculae and median line weakly developed; endostome yellow, papillose throughout, basal membranes short, barely exceeding the capsule mouth, segments linear, to 500 µm long, weakly and narrowly perforate, not keeled, cilia absent. Spores irregularly rounded, 16–23 µm, lightly papillose. Calyptrae mitrate, lobed, ramentose, to 1 mm long.

Illustrations. Brotherus (1925, Fig. 571); Bartram (1949, Fig. 125 D–F); Breen (1963, Pl. 105 6–9); Florschütz (1964, Fig. 107); Crum and Anderson (1981, Fig. 386); Florschütz-de Waard (1986,

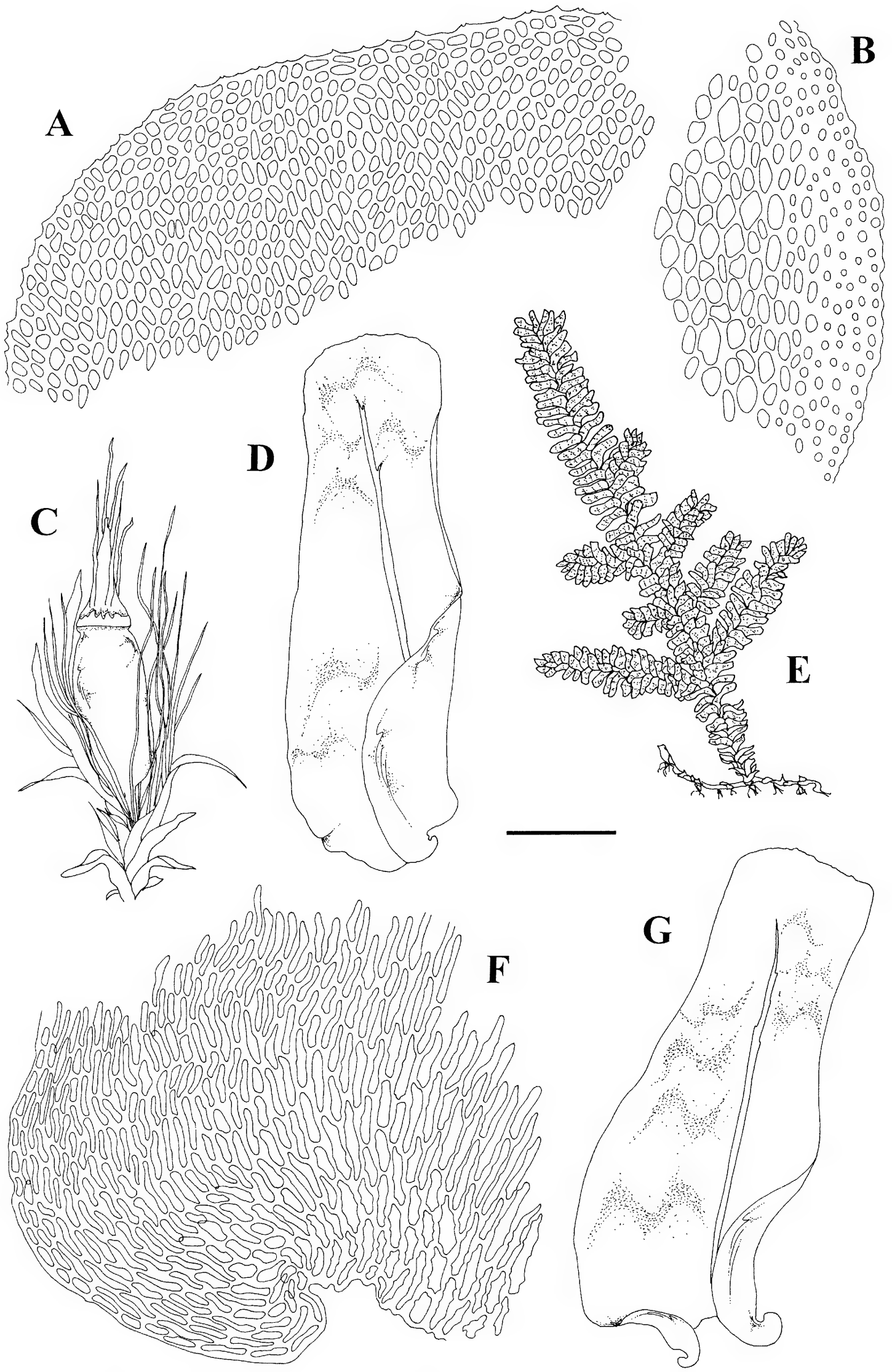


Figure 97. *Neckeropsis undulata*. A. Leaf apex. B. Stem in cross section. C. Capsule, calyptra, and paraphyses. D & G. Leaves. E. Habit. F. Basal and alar cells. Scale in mm: bar = 0.06 (A, B, F); bar = 0.5 (D, G); bar = 1.0 (C); bar = 6.7 (E). C, E from *Liesner 26291*; all other figure parts from *Allen 17621*.

Fig. 107); Sharp *et al.* (1994, Fig. 552); Churchill and Linares (1995, Fig. 132 a–e); Duarte Bello (1997, Pl. 213); Buck (1998, Pl. 40 1–8); Gradstein *et al.* (2001, Fig. 159 K–Q); Buck (2003, Fig. 106 A–H). Figure 97.

Habitat. On tree trunks, branches, twigs, and vines, fallen logs, and occasionally on rocks and boulders; sea level–1880 m.

Distribution in Central America. BELIZE. Cayo: *Allen 18209* (MO); Orange Walk: *Mann 34* (NY); Stann Creek: *Gentle 2157* (F, NY); Toledo: *Allen 18561A* (MO). GUATEMALA. Alta Verapaz: *Johnson 338* (NY, US); Izabal: *Steyermark 41813* (F, FH); Petén: *Lundell 2935* (FH, MO, NY, US). HONDURAS. Atlántida: *Allen 17621* (MO, TEFH); Copán: *Allen 17692* (MO); Cortés: *Allen 14148* (MO); Olancho: *Allen 12792* (MO). NICARAGUA. Chontales: *Standley 9004* (F); Estelí: *Granzow de la Cerda GC-1580* (DUKE, MO); Jinotega: *Stevens 16469A* (MO); Managua: *Standley 8406* (F); Matagalpa: *Richards et al. 3720c* (F); Zelaya: *Danin 2-C* (MO). COSTA RICA. Alajuela: *Burger et al. 11638C* (F); Cartago: *Standley & Valerio 47153b* (FH); Guanacaste: *Dauphin 1853* (MO); Heredia: *Godfrey 65591* (MO); Limón: *Steere CR-84* (NY); Puntarenas: *Crosby 3826* (MO); San José: *Alfaro 147* (FH, US). PANAMA. Bocas del Toro: *Allen 5818* (MO); Canal Area: *Dodge 16604* (MO); Chiriquí: *Crosby 3957* (MO); Coclé: *Hunter & Allen 432* (MO); Colón: *Crosby 10355* (MO, PMA); Darién: *Allen 8658A* (MO); Panamá: *Crosby 4549A* (MO), San José Island: *Johnson s.n.* (F, FH, NY); San Blas: *Allen 4971* (MO); Veraguas: *Crosby 10267* (MO, PMA).

World range: Southeastern U.S.A.; Mexico; Central America; Caribbean; Western, Northern and Southern South America, Brazil.

Neckeropsis undulata is the most common species of *Neckeropsis* in Central America. It is usually a medium-sized to large species, with plants that are often tinged with an intense blackish color, and leaves that are strongly undulate when both wet and dry. Its leaves are truncate across the apex, with long, single, often forked costae and cordate to auriculate leaf bases. Its capsules are immersed and surrounded by numerous ramenta. The ramentose perichaetia in this species develop very soon after fertilization and reach their maximum length before the vaginulae and calyptra separate (Touw 1962). As a result, they can be recognized before the perichaetia show evidence of sporophyte development. The development of the sporophyte in *N. undulata* is accompanied by the formation of a pseudopodium, which raises the sporophyte away from the stem or branch. The calyptrae of *N. undulata* are mitrate and deeply lobed. All Central American material of *N. undulata* had calyptrae covered with ramenta, but Sastre (1987) and Buck (1998) indicate the calyptrae can sometimes be naked.

Neckeropsis fovelata is very similar to *N. undulata.* It differs from *N. undulata* only in lacking perichaetial ramenta and in having longer (3.5–4.5 mm vs. 1.5–2.8 mm) perichaetial leaves that consistently overtop the operculate capsules. *Neckeropsis disticha* is similar to *N. undulata* in having pseudopodium development and numerous perichaetial ramenta. It differs from *N. undulata* in having non-auriculate leaves that are smooth to crisped when dry and flat when wet. Furthermore, the apical leaf cells of *N. disticha* are shorter than those of *N. undulata*, and it has naked, cucullate calyptrae.

Sastre (1987) considered *N. undulata* close to the Southeast Asian *N. crinata* (Griff.) M. Fleisch., which seems to differ only in having somewhat smaller leaf cells and shorter, broader capsules.

6. *Orthostichella* Müll. Hal., Bull. Herb. Boissier 5: 204. 1897.

Neckera sect. *Pseudopilotrichum* Müll. Hal., Syn. 2: 123. 1850. *Pseudopilotrichum* (Müll. Hal.) W. R. Buck & B. H. Allen *in* W. R. Buck, J. Hattori Bot. Lab. 75: 69. 1994.
Neckera sect. *Pseudopilotrichum* subsect. *Orthostichella* Müll. Hal., Syn. 2: 123. 1850.

Plants slender or medium-sized, dull, yellow green, reddish yellow, or brownish red, in dense or loose mats often with pendent strands. Stolons red, creeping; rhizoids on stolons, at base of stipitate stems, or on flagelliform branch tips, red, not or irregularly branched, from clusters of initials abaxial to the leaf insertions; leaves widely spaced, reduced, erect, broadly ovate or ovate-triangular, abruptly long-pointed, ecostate or costa short and double. Stems occasionally stipitate, horizontal or erect, frequently and irregularly branched, at times with flagelliform tips, yellowish green, becoming dark red with age; stems in cross section with sclerodermis, enlarged cortical cells, central strand absent; paraphyllia and pseudoparaphyllia absent, scale leaves present; axillary hairs 3–4 cells long,

basal cell quadrate to subquadrate, reddish brown, upper 2–3 cells broadly cylindrical, hyaline or reddish. Stipe leaves ovate-piliferous, auriculate, cordate, rounded at base or straight to the insertions. Stem and branch apices turgid; stem leaves not or rarely seriately ranked, ovate, erect, variously clasping below, rounded to the base, abruptly narrowly acuminate, at times hair-pointed; branch leaves weakly ranked when dry, distinctly seriate ranked when wet, leaves panduriform, broadly oblong, obovate, oblong-obovate, or broadly obovate, erect to erect-spreading, appressed and at times clasping below, abruptly flexed and spreading above, stem leaves often auriculate, apex abruptly acuminate, cuspidate to long-cuspidate; margins broadly incurved, sharply serrulate above, plane or broadly incurved, serrulate below, entire or weakly toothed on basal auriculation; costae short double, short single, long single, or absent; leaf cells long-flexuose, smooth to slightly porose, outer basal cells shorter and broader, inner basal cells elongate, porose; alar cells subquadrate to short-rectangular, extending up the margins in 2–4 rows and across the insertion in 2–4 rows, yellow across the insertions. Asexual reproduction by deciduous leaves. Dioicous. Perigonia gemmiform, lateral on secondary stems and branches. Perichaetia lateral; leaves lanceolate, vaginulae often densely hairy. Setae short, wavy, smooth below, roughened above, yellow. Capsules exserted, erect to somewhat inclined, ovoid to short-cylindrical, neck moderately developed; exothecial cells small, rounded in several rows below the mouth, subquadrate, irregularly short-rectangular, or oblate, firm-walled below, cells in neck smaller than the median cells; stomata superficial on neck; opercula obliquely long-rostrate; annuli rudimentary, of 2–3 rows of thin-walled enlarged cells; peristome yellowish white; exostome teeth linear, dorsal (outer) surface horizontally striate at base, smooth or finely papillose above, trabeculae weakly developed on both sides; endostome nearly as long as exostome, basal membranes very low, segments filamentous, narrowly perforate, not keeled, smooth to papillose, cilia rudimentary or absent. Calyptrae cucullate, hairy or smooth.

Orthostichella is a genus of predominantly epiphytic, frequently pendulous mosses of tropical and subtropical American-African distribution. Plants of *Orthostichella* have creeping primary stems and erect or pendent secondary stems. Its stolons, stems, and branches lack a stem central strand, and its axillary hairs are usually reddish throughout. The secondary stems can be strongly stipitate or non-stipitate throughout; at times both types of secondary stems can be found on the same primary stems. Its branches often end in filiform attenuations or stolons. The stolons, secondary stems, branches, and filiform attenuated branches can be morphologically distinct, but more often they intergrade or abruptly transform from one structure to another. In general the leaves on the branches (and sometimes the secondary stems) are spirally ranked, while those on the stolons and primary stems are unranked. Most leaves are cuspidate, with distinctive incurved, serrulate upper leaf margins, elongate, smooth, firm-walled leaf cells, and weakly developed, reddish yellow, firm-walled alar cells. The costae in *Orthostichella* are one of its oddest features. In some species, most leaves are ecostate, but here and there leaves with short double, short single, or long single costae can be found. In other species, most leaves have a long single or long double costa, but here and there ecostate leaves can be found.

Orthostichella is a dioicous genus and sporophytes are rarely encountered. They are, however, uniform throughout the genus. The setae are elongate-flexuose and variously papillose, roughened above. The genus has ovoid to short-cylindrical capsules, long-rostrate opercula, and mostly hairy, cucullate calyptrae. *Orthostichella* has a reduced, diplolepideous peristome, with yellowish white exostomes and endostomes that are nearly the same length as the exostome teeth. The more or less linear exostome teeth are lightly horizontally striate on the dorsal (outer) surface at base. The endostome has a low basal membrane with filamentous, narrowly perforate segments; cilia are usually absent. *Orthostichella* essentially has a neckeroid peristome, but the presence at the base of the exostome teeth of horizontal striae indicates it likely represents a reduced, hypnoid-type peristome.

The genus has long been treated as a subgroup of *Pilotrichella* (Müll. Hal.) Besch. (Fleischer 1908; Brotherus 1925; Bartram 1949; Florschütz 1964; Walther 1983; Vitt 1984; Spessard-Schueth 1994b; Churchill & Linares 1995; Duarte Bello 1997; Magill & Rooy 1998). *Pilotrichella* differs from *Orthostichella* in its larger plant size; absence of stipitate stems; and non-ranked, absolutely ecostate leaves with well-developed alar cells. Sporophytically, *Pilotrichella* differs from *Orthostichella* in having longer setae and larger (to 64 μm) spores. Although *Orthostichella* has been placed in the Lembophyllaceae (Buck 1994a, 1994b), a recent revision of the genus (Allen & Magill 2007)

considered it better placed in the Neckeraceae by virtue of its stolon/stipe morphology, poorly and variably developed leaf costae, and yellowish white neckeroid peristome. Within the Neckeraceae, the genus is isolated by virtue of its non-complanate stems with leaves that are often arranged in spiral rows.

The name *Orthostichella* combines the Greek *orthos* (straight) and *stichos* (row) with the Latin substantival suffix *-ella* (diminutive). The name refers to the strongly ranked branch leaves in the genus; they are, however, often in spiral rather than straight rows.

1. Branch leaves not or somewhat rounded to the insertions . . . . . 3. *O. versicolor*
1. Branch leaves strongly rounded to auriculate at the insertions 2

2. Plants with deciduous leaves . . . . . 1. *O. pachygastrella*
2. Plants without deciduous leaves . . . . . 2. *O. rigida*

1. *Orthostichella pachygastrella* (Müll. Hal. *ex* Ångstr.) B. H. Allen & Magill, Bryologist 110: 16. 2007. *Pilotrichella pachygastrella* Müll. Hal. *ex* Ångstr., Ofvers. Forh. Kongl. Svenska Vetensk.-Akad. 33(4): 33. 1876. Protologue. [Brazil] Regnell No 3b et Henschen. Types. Brasilia, *A. F. Regnell n^{o} 3^{b}* (S, lectotype); Caldas, *Regnell n^{o} 3^{b}* (H, S, isolectotypes); Caldas Brasiliae, *S. Henschen* (BM, S, syntypes).

Pilotrichella cyathipoma (Müll. Hal.) Kindb. var. *laxiretis* Herzog, Biblioth. Bot. 87: 112. 1916. Protologue. [Bolivia] An Bäumen im Wald des Randgebirges bei Yacuiba, ca. 500 m, [*Herzog*] *No. 2626*. Types. Bolivia. Im Wald des Randgebirges bei Yacuiba, ca. 500 m, Oktober 1910, *Th. Herzog No. 2626* (JE, holotype; H, L, S, isotypes).

Plants slender to medium-sized, dull, light green, yellow green, reddish yellow, or brownish green, in loose mats often with pendent strands. Stolons yellow to red, creeping; rhizoids on stolons, at base of stipitate stems, or on flagelliform branch tips, red, not or irregularly branched, from clusters of initials abaxial to the leaf insertions; leaves widely spaced, reduced, erect, ovate-triangular, abruptly acuminate, ecostate, 1.0–1.4 mm long. Stems stipitate or nonstipitate, horizontal, erect or pendent, frequently and irregularly branched, branches at times with flagelliform tips, 4–10(–40) cm long, yellowish green, becoming dark red with age; stems in cross section with sclerodermis of 3–5 small, thick-walled, yellowish to reddish orange cells, cortical cells enlarged, firm-walled, pale yellow, red with age, central strand absent; paraphyllia absent, pseudoparaphyllia absent, scale leaves present; axillary hairs 2–3 cells long, basal cell quadrate to subquadrate, reddish brown, upper 1–2 cells broadly cylindrical, red. Stipe leaves ovate, cordate, rounded to the insertions. Stem and branch apices turgid; stem and branch leaves differentiated only in size, stem leaves not or obscurely ranked when dry, branch leaves often distinctly seriately ranked when dry or wet, leaves obovate to oblong-obovate, erect to erect-spreading, variously clasping below, 1.0–1.2 mm long, auriculate, apex cuspidate; margins broadly incurved and sharply serrulate above, plane or broadly incurved, serrulate or entire below; costae mostly absent, occasionally short double or short single; leaf cells long-flexuose, smooth, upper cells 20–40 × 4–6 µm, median cells 30–60 × 3–4 µm, outer basal cells shorter and broader, inner basal cells near insertion elongate, often porose; alar cells red to red yellow, subquadrate to short-rectangular, not reaching the outer margins or extending up the margins, cells across the insertions yellow. Asexual reproduction by deciduous leaves. Dioicous. Perigonia gemmiform, lateral on secondary stems and branches, 0.8–1.2 mm long; leaves ovate, acuminate. Perichaetia lateral, 1.4–2.0 mm long; leaves lanceolate, vaginulae moderately hairy. Setae short, wavy, 3–5 mm long, smooth below, roughened above, yellow, becoming yellowish red with age. Capsules exserted, erect to somewhat inclined, ovoid to short-cylindrical, 1.0–1.5 mm long, neck moderately developed; exothecial cells small, rounded in 2–3 rows below the mouth, subquadrate, irregularly short-rectangular, or oblate, firm-walled below, cells in neck smaller than the median cells; stomata superficial on neck; opercula obliquely long-rostrate, 1.0–1.5 mm long; annuli rudimentary, of 2–3 rows of thin-walled enlarged cells; peristome yellowish white; exostome teeth linear, dorsal (outer) surface lightly horizontally striate at base, smooth or finely papillose above, trabeculae weakly developed on both sides; endostome nearly as long as exostome, basal membranes very low, segments filamentous, narrowly

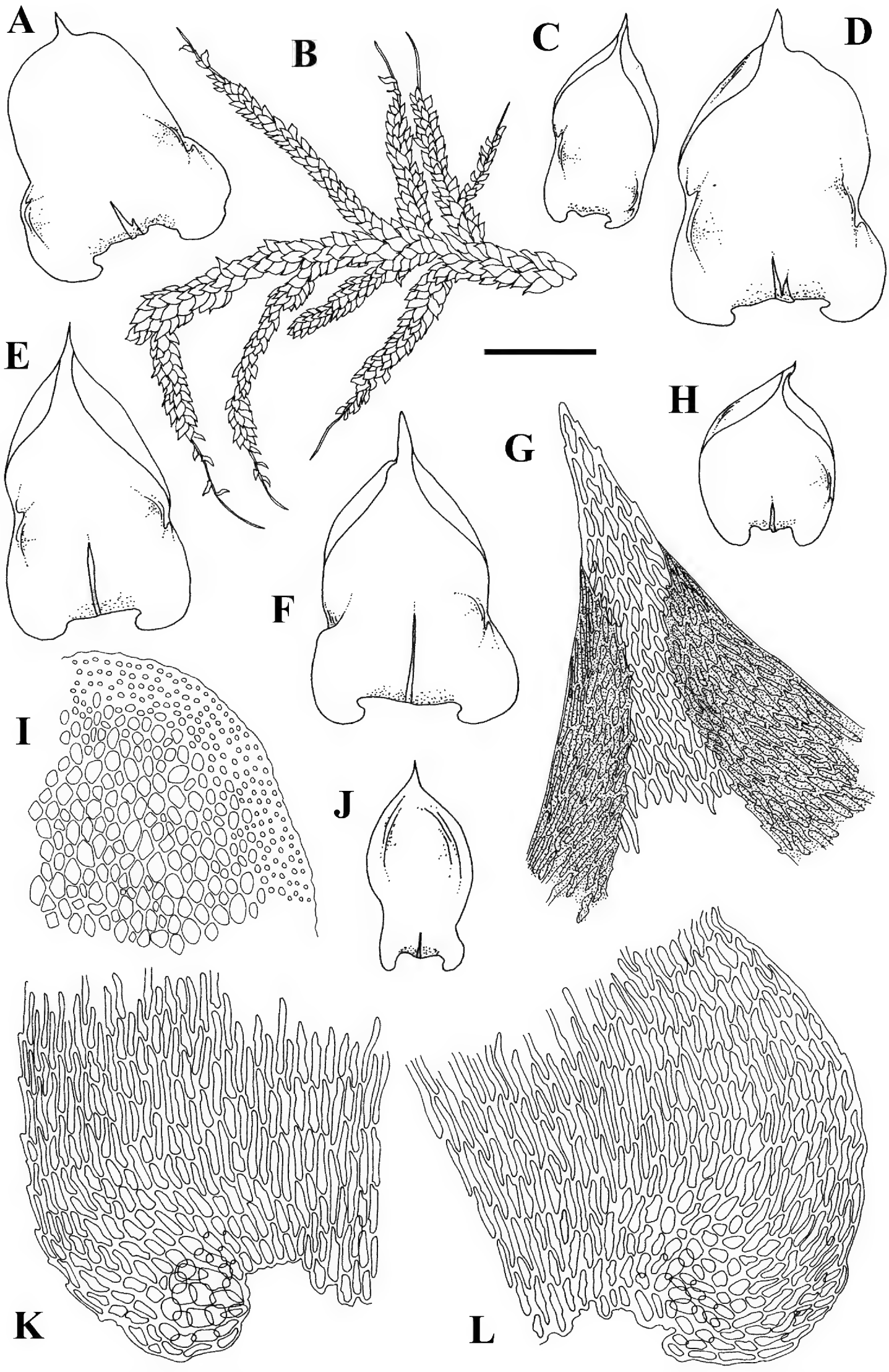
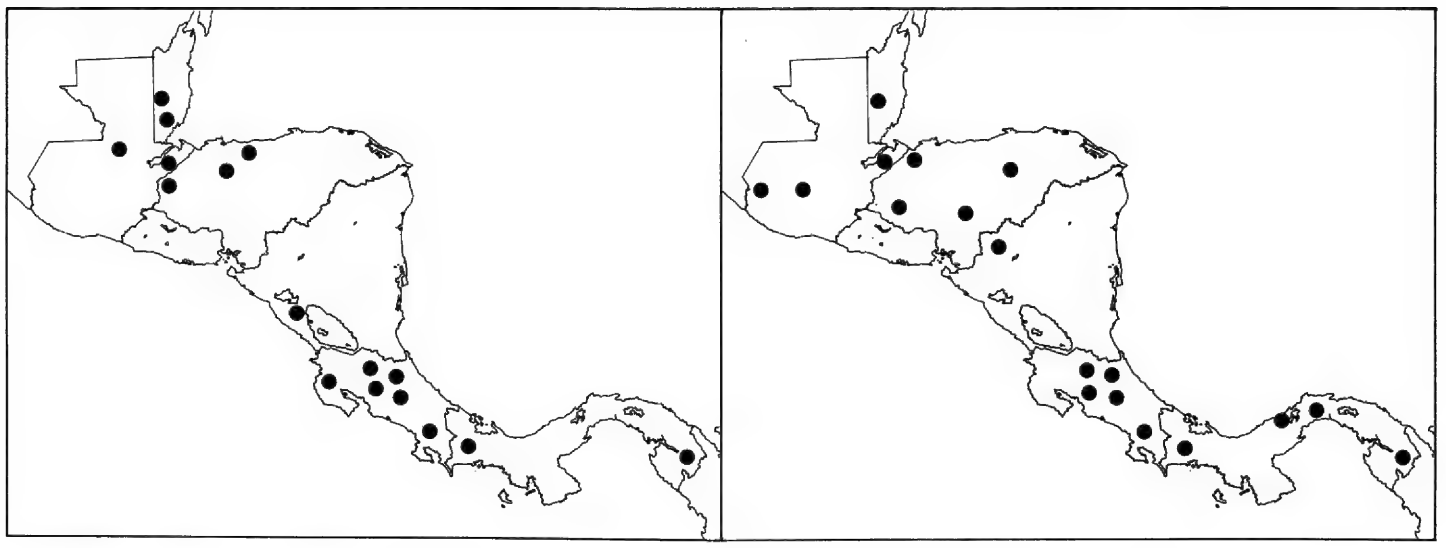


Figure 98. *Orthostichella pachygastrella*. A. Stipe leaf. B. Habit. C, H & J. Branch leaves. D–F. Secondary stem leaves. G. Leaf apices. I. Stem in cross section. K & L. Leaf basal angles. Scale in mm: bar = 0.06 (G, K, L); bar = 0.08 (I); bar = 0.4 (A, C–F, H, J); bar = 3.2 (B). All figure parts from *Zardini 39949*.



Orthostichella pachygastrella *Orthostichella rigida*

perforate, not keeled, smooth to papillose, cilia rudimentary or absent. Spores round, lightly roughened, 14–20 µm long. Calyptrae 2.0–2.5 mm long, narrowly cucullate, lightly hairy.

Illustrations. Allen and Magill (2007, Fig. 6). Figure 98.

Habitat. On tree trunks, fallen branches, and logs, pendent from shrubs, tree fern fronds, vines, and twigs, occasionally on boulders; 150–3200 m.

Distribution in Central America. BELIZE. Toledo: *Allen 18679* (MO); Cayo: *Allen 15151* (MO). GUATEMALA. Alta Verapaz: *Steyermark 45072* (MO); Izabal: *Steyermark 39991* (MO). HONDURAS. Atlántida: *Allen 17576* (MO, TEFH); Copán: *Allen 17781* (MO); Yoro: *Allen 13646* (MO). NICARAGUA. Granada: *Almedo 1459b* (MO). COSTA RICA. Alajuela: *Bowers 389-b* (MO); Cartago: *Liesner 14347* (MO); Guanacaste: *Standley & Valerio 45533* (FH, H); Heredia: *Crosby 10865* (MO); Puntarenas: *Lyon 511* (CR, MO); San José: *Crosby & Crosby 6203* (MO). PANAMA. Chiriquí: *Cornman 3183* (MO); Darién: *Hammel et al. 16272* (MO).

World range: Mexico; Central America; Western and Southern South America, Brazil.

Orthostichella pachygastrella is a slender species; it often has a stipitate habit and regularly branched stems. The species is especially common in southeastern South America, absent in northern Southern America, but present from southern Mexico to Panama. The stem leaves of *O. pachygastrella* are erect and clasping at base, but the branch leaves are typically in spiral rows and mostly erect at base. *Orthostichella pachygastrella* differs from all other New World species of *Orthostichella* in having consistently deciduous leaves; nearly all collections have at least some fully denuded branches. The stem leaves of *O. pachygastrella* are auriculate at base and can be long-cuspidate, while the branch leaves are mucronate to short-cuspidate and rounded at base. The stem and branch leaves can be ecostate or have weak single or double costae.

Orthostichella capillicaulis (Müll. Hal. *ex* Kindb.) B. H. Allen & Magill is the only other *Orthostichella* species with consistently deciduous leaves, and both species have auriculate stem leaves. It is, however, an African species that further differs from *O. pachygastrella* in having long-cuspidate stem and branch leaves as well as branch leaves that are auriculate rather than rounded at base. *Orthostichella rigida* and *O. muelleri* (Dusén) B. H. Allen & Magill are similar to *O. pachygastrella* in having auriculate stem leaves. Both species, however, have non-deciduous leaves. *Orthostichella muelleri* is primarily a west African species also present in western South America. It also differs from *O. pachygastrella* in having julaceous stems with leaves that are extremely clasping at base, and auriculate branch leaves.

2. *Orthostichella rigida* (Müll. Hal.) B. H. Allen & Magill, Bryologist 110: 25. 2007. *Neckera rigida* Müll. Hal., Syn. Musc. Frond. 2(1): 126. 1850. *Pilotrichella rigida* (Müll. Hal.) Besch., Mém.

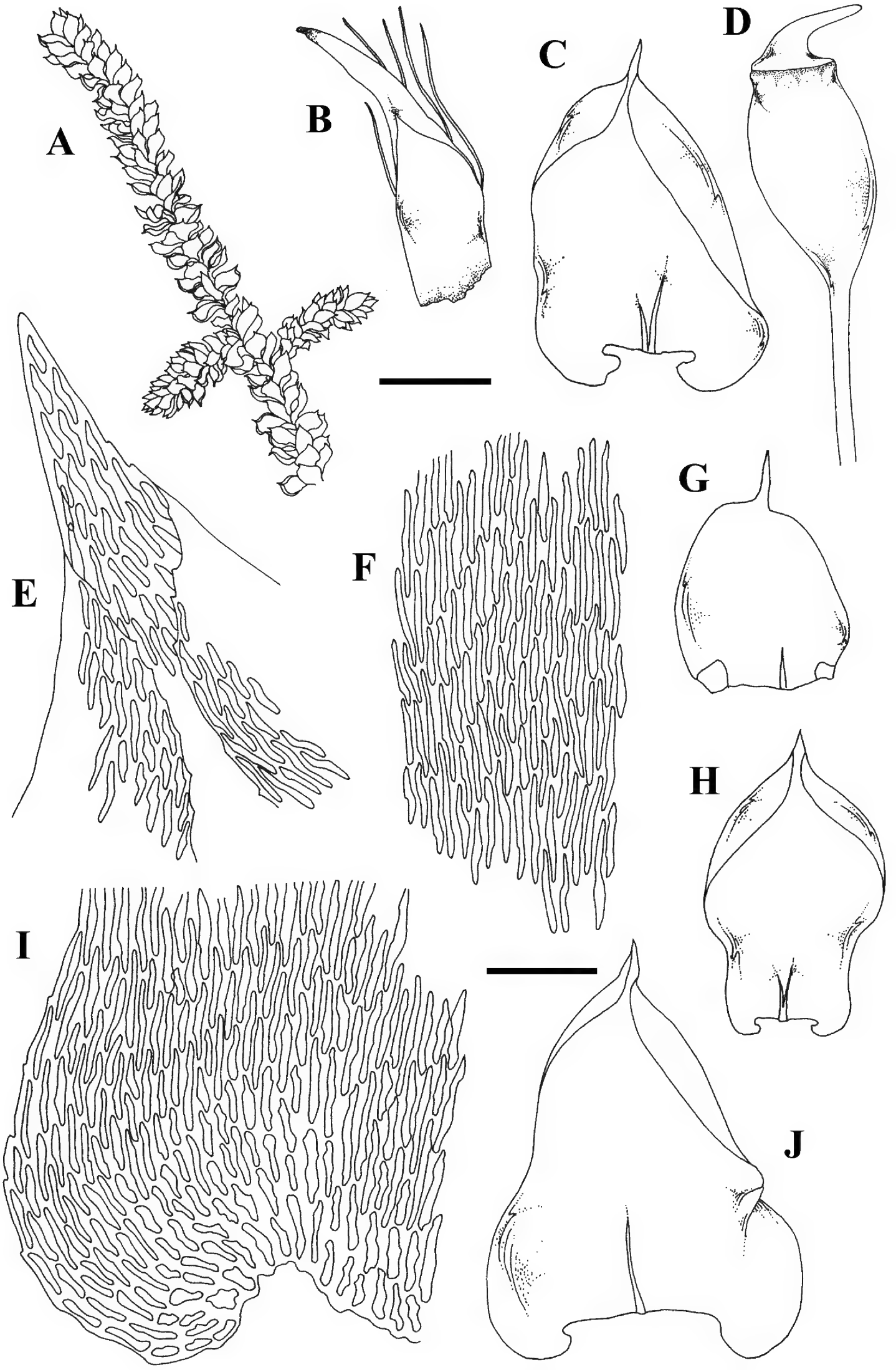


Figure 99. *Orthostichella rigida*. A. Habit. B. Calyptra. C. Secondary stem leaf. D. Seta, capsule, and operculum. E. Leaf apex. F. Median leaf cells. G. Stolon leaf. H. Branch leaf. I. Leaf basal angle. J. Stipe leaf. Scale in mm: bar = 0.05 (E, F, I); bar = 0.4 (C, G, H, J); bar = 0.6 (B, D); bar = 2.5 (A). A from *Crosby 8980*; B, D from *Magill 13788*; C from *Quintas*; G from *Crosby & Crosby 9119*; J from *Miquel* (type); all other figure parts from *Hildebrandt*.

Soc. Sci. Nat. Cherbourg 16: 222. 1872. Protologue. Mexico: Hb. *Miquel*, *Deppe*. Type. Mexico, *Miquel* (BM, lectotype).

Pilotrichella mexicana Schimp. *ex* Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 223. 1872. Protologue. Mejico (*F. Müller*, Schimper comm.). Types. Herbarium Mexicanum, A?. 1853. *Fred. Müller*. Comm. H. Schlumber. [Herb. Bescherelle] (BM, holotype); Orizaba, lg. *F. Müller* (BM, isotype).

Pilotrichella pulchella Schimp. *ex* Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 222. 1872. Protologue. Mexico. Orizaba (*F. Müller*, Lorentz mihi comm.). Types. Mexico. Orizaba, 1853, legit *F. Müller* [Herb. Bescherelle] (BM, holotype); Mexico, Orizaba, leg. *Müller 1853* (H, isotype).

Neckera ampullacea Hampe *ex* Müll. Hal., Linnaea 40: 264. 1876. *Pilotrichella ampullacea* (Müll. Hal.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 256. 1877. Protologue. Comoro Islands. Comoro–insula Johanna, ubi primum legit *Prof. Peters Berol.* 1843; inter alios muscos misit *J. M. Hildebrandt* 1875. Types. In mont. Ins. St. Johann (Comores), leg *Hildebrandt* [Herb. Hampe] (BM, lectotype); In mont. Ins. St. Johann, leg *Hildebrandt* [Herb. Hampe] (BM, isolectotype); Africa: Comoro – insula Johaña. leg. *Hildebrandt*, 1875 (H, isolectotype).

Plants slender, dull, yellow green, reddish yellow, or brownish red, in dense mats. Stolons red, creeping; rhizoids only on stolons, red, not or irregularly branched, from clusters of initials abaxial to the leaf insertions; leaves widely spaced, reduced, erect, broadly ovate, abruptly long-pointed, ecostate or costa short and double, 0.6–0-8 mm long. Stems occasionally stipitate, horizontal or erect, frequently and irregularly branched, at times with flagelliform tips, to 5 cm long, yellowish green, becoming dark red with age; stems in cross section with sclerodermis of 3–5 small, thick-walled, reddish orange cells, cortical cells enlarged, firm-walled, pale yellow, red with age, central strand absent; paraphyllia absent, pseudoparaphyllia absent, scale leaves present; axillary hairs 3–4 cells long, basal cell quadrate to subquadrate, reddish brown, upper 2–3 cells broadly cylindrical, hyaline or reddish. Stem and branch apices turgid; stem and branch leaves differentiated only in size, obscurely seriately ranked when dry, distinctly so when wet; leaves panduriform, broadly oblong, appressed and clasping below, broadly obovate, abruptly flexed and spreading above, stem leaves 1.0–1.5 mm long, strongly auriculate; apex abruptly acuminate, long-cuspidate, cusp 80–140 µm long; margins broadly incurved, sharply serrulate above, plane or broadly incurved, serrulate below, weakly toothed on basal auricles; costae short-double, short-single, or absent; leaf cells long flexuose, smooth to slightly porose, 18–40 × 3–5 µm, outer basal cells shorter and broader, inner basal cells elongate, porose; alar cells subquadrate to short-rectangular, extending up the margins in 2–4 rows and across the insertion in 2–4 rows, yellow across the insertion. Dioicous. Setae short, wavy, 2–3 mm long, smooth below, roughened above, yellow. Capsules exserted, erect to somewhat inclined, ovoid to short-cylindrical, 1.0–1.5 mm long, neck moderately developed; exothecial cells small, rounded in 2–3 rows below the mouth, subquadrate, irregularly short-rectangular, or oblate, firm-walled below, cells in neck smaller than the median cells; stomata superficial on neck; opercula obliquely long-rostrate, 1.5 mm long; annuli rudimentary; peristome yellowish white; exostome teeth linear, 0.5–0.6 mm long, dorsal (outer) surface horizontally striate at base, smooth or finely papillose above, trabeculae weakly developed on both sides; endostome nearly as long as exostome, basal membranes very low, segments filamentous, narrowly perforate, not keeled, smooth to papillose, cilia rudimentary or absent. Spores round, lightly roughened, 17–26 µm long. Calyptrae 2 mm long, cucullate, hairy.

Illustrations. Dusén (1895, p. 33 a & b; 3f 1); Allen and Magill (2007, Fig. 8). Figure 99.

Habitat. On tree trunks, branches, twigs, and roots, vines, logs, and on shaded rocks; 350–3175 m.

Distribution in Central America. BELIZE. Cayo: *Allen 18112* (MO). GUATEMALA. Chimaltenango: *Wenzel & Mitchell* (F, MO); Izabal: *Steyermark 41792* (F, FH, MO); San Marcos: *Croat 40907* (MO). HONDURAS. Cortés: *Allen 14354* (MO, NY); Francisco Morazán: *Allen 12389B* (MO); Lempira: *Allen 11938* (MO); Olancho: *Allen 12778* (MO). NICARAGUA. Madriz: *Stevens 16137* (HNMN, MO). COSTA RICA. Alajuela: *Crosby & Crosby 5754* (BM, CR, G, H, MO, NY, US); Cartago: *Liesner & Judziewicz 14515* (MO); Heredia: *Crosby & Crosby 5780* (BM, CR, F, FH, G, H, JE, NY, S, US); Puntarenas: *Lyon 511* (CR, MO); San José: *Crosby & Crosby 5746* (BM, CR, F, FH, G, H, JE, MICH, NY, PC, S, US). PANAMA. Chiriquí: *Mori & Bolten 7152b* (MO); Colón: *Crosby 10452* (F, FH, MO, NY); Darién: *Allen 8753* (MO); Panamá: *Crosby 4489* (MO).

World range: Mexico; Central America; Western and Northern South America; Brazil; West-Central and East Tropical Africa, Western Indian Ocean.

Orthostichella rigida is a fairly common species in Central America, and it is the most common species of *Orthostichella* across tropical Africa. The stems of *O. rigida* are often branched close to the stolons, and as a result the plants usually form compact mats and seldom exhibit a stipitate habit. The species has closely spaced, panduriform stem and branch leaves that are appressed, clasping below and abruptly flexed and spreading above. The stem as well as the branch leaves are auriculate to strongly rounded at base, and the basal margins are often weakly toothed. The costae of *O. rigida* are consistently weak, and the alar cells are poorly developed. Although African collections of *O. rigida* are extremely variable in morphology and overall size, New World populations are much more stenotypic. For example, African collections of *O. rigida* sometimes have long-cuspidate stem and stolon leaves, but New World collections have consistently mucronate or short-cuspidate branch leaves. In size and aspect *O. rigida* is sometimes nearly identical to the Caribbean *O. hexasticha* (Schwägr.) W. R. Buck, and both species have the same leaf stance. *Orthostichella hexasticha* differs from *O. rigida* in having stem leaves that are less rounded to the insertion and never strongly auriculate.

The most troubling expression of *Orthostichella rigida* is one in which the branch leaves are only weakly rounded at base. The expression is quite similar in size to *O. versicolor*, and both species have expressions with closely intergrading leaf forms. The similarity between the two can be so close that many collections are almost impossible to place. Fortunately this troublesome expression is not nearly as common in Central America as in Africa and northern South America. *Orthostichella versicolor* differs from *O. rigida* in having non-clasping branch leaves that are erect rather than appressed and so weakly rounded at base that the alar cells reach the outer margins of the leaves.

The oldest name associated with *Orthostichella* is *Hypnum imbricatum* P. Beauv. Allen and Magill (2007) were unable to locate the type of this name, which was collected by Bory-St. Vincent on Réunion. There are only two species of *Orthostichella* known from Réunion, *O. rigida* and *O. longinervis*; *Hypnum imbricatum* predates both of them. Although *O. rigida* agrees more closely than *O. longinervis* with the scant protologue of *Hypnum imbricatum*, it is possible that *H. imbricatum* is an *Orthostichidium.* Until the type is located and examined the deposition of the name remains uncertain.

3. *Orthostichella versicolor* (Müll. Hal.) B. H. Allen & W. R. Buck, Mem. New York Bot. Gard. 76(3): 140. 2003. *Neckera versicolor* Müll. Hal., Syn. Musc. Frond. 2(1): 127. 1850. *Orthostichella versicolor* (Müll. Hal.) Hampe, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn, ser. 3, 2: 277. 1870, combination invalid. *Pilotrichella versicolor* (Müll. Hal.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 258. 1877. Protologue. Brasilia, Rio Janeiro: *Beyrich, Beske*. Types. Brasilia, Serra d'Estrella, *Beyrich* (BM, lectotype); Serra d'Estrella et Nov. Friburg, ad radices arborum, *Beyrich* (BM, isolectotype).

Neckera viridis Müll. Hal., Syn. Musc. Frond. 2(1): 125. 1850. *Pilotrichella viridis* (Müll. Hal.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 258. 1877. *Orthostichella viridis* (Müll. Hal.) Müll. Hal., Linnaea 42: 493. 1879, combination invalid. Protologue. Venezuela, Caracas: *Moritz*. Coll. *I. Thorreyana Hamburgensis No. 38*. Types. Caracas, leg. *Moritz No. 38* (BM, lectotype); Caracas, *Moritz 38* (L, isolectotype); Venezuela, Caracas, *Moritz*, Müller in Hb. (NY, isolectotype).

Neckera pachygaster Müll. Hal., Syn. Musc. Frond. 2(1): 126. 1850. *Pilotrichella pachygaster* (Müll. Hal.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 256. 1877. Protologue. Venezuela, in montibus nivosis prov. Meridae: *Moritz*. Types. Caracas. leg. *Moritz 171. Neckera pachygaster* CM., Columbien (Merida 1844/45) (BM, lectotype); Columbien, Merida, 1844/45, leg. *Moritz 171* (H, isolectotype), Merida, *Moritz 171* (L, isolectotype).

Neckera pachygaster var. *gracilis* Müll. Hal., Bot. Zeitung (Berlin) 15: 582. 1857. *Pilotrichella pachygaster* var. *gracilis* (Müll. Hal.) Paris, Index Bryol. 948. 1897. Protologue. [Colombia] Nova Granada, S. Martha, Mina, 4000 ped. alta: *Funck et Schlim* in Coll. Linden No. 1034. Types. Nova Granada, S. Martha, Mina, 4000 ped., leg. *Funck & Schlim* (BM, lectotype); Voyage de L. Schlim. N^{lle} Grenade, prov. de Santa Marta. Hauteur 4000 fts. Minca, 1846 à 1852 fl. en Mai, *N^{o} 1043* (L, probable isolectotype).

Orthostichella filamentosula Müll. Hal., Bull. Herb. Boissier 5: 204. 1897. *Pilotrichella filamentosula* (Müll. Hal.) Paris, Index Bryol. Suppl. 271. 1900. Protologue. Guatemala. Sine loco speciali quam linteum in-

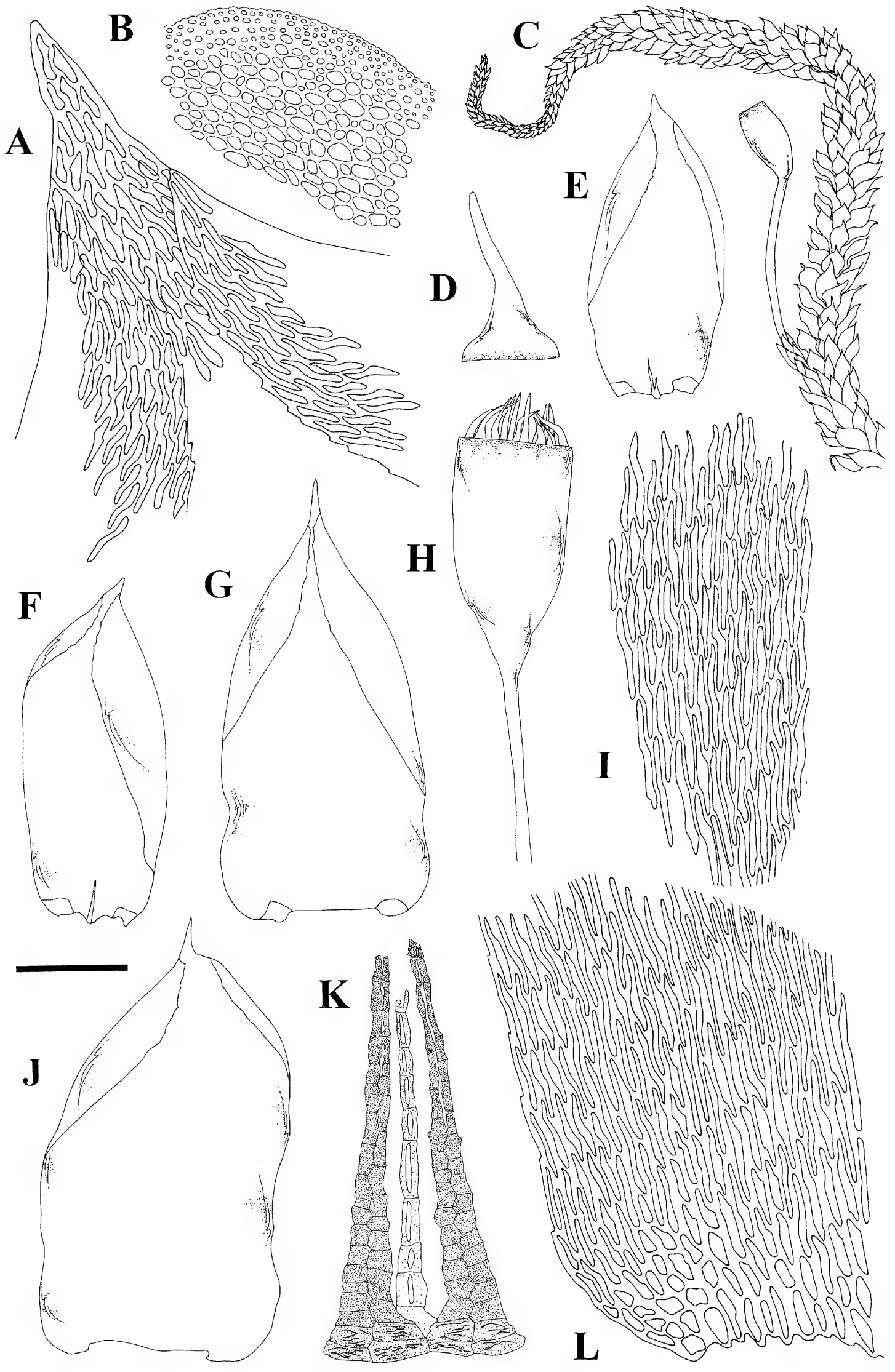
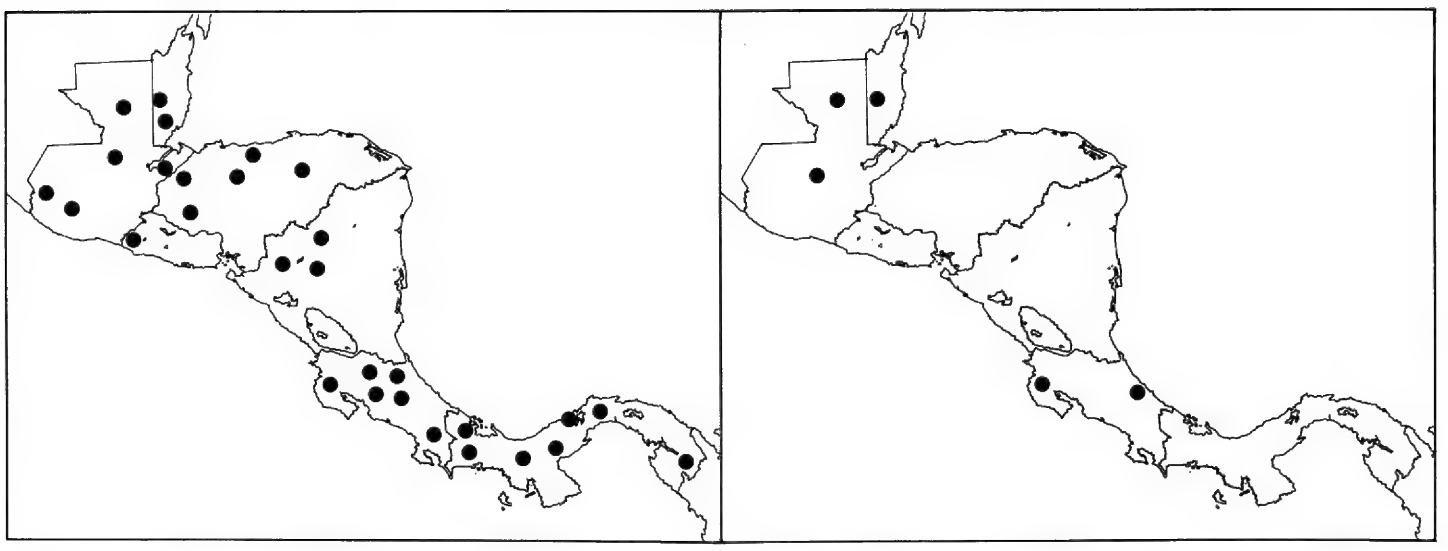


Figure 100. *Orthostichella versicolor*. A. Leaf apex. B. Stem in cross section. C. Habit. D. Operculum. E & F. Branch leaves. G & J. Stem leaves. H. Sporophyte. I. Median leaf cells. K. Peristome. L. Leaf basal angle. Scale in mm: bar = 0.05 (A, I, L); bar = 0.08 (B, K); bar = 0.26 (E–G, J); bar = 0.6 (D, H); bar = 1.56 (C). A, I from *Allen 18428*; B from *Allen 18023*; C from *Allen 12148*; D, H, K from *Crosby 9921*; all other figure parts from *Beyrich* (type).



Orthostichella versicolor *Pinnatella minuta*

volucris serviens (Packmaterial) in Museo zoologico Florentino 1892: Hb. Levier. Types. e viciniis urbis Guatemala. rudem accepit Mus. Zoolog. Florent. quam involucrum animalium, 1892, legit *indigenus* (BM, lectotype); e viciniis urbis Guatemala. rudem accepit cum pellibus animalium Mus. Zool. Florentinum, 1892, *collector ignotus* (H, NY, isolectotypes).

Pilotrichella angustifolia Herzog, Biblioth. Bot. 87: 112. 1916. Protologue. [Bolivia] Ad Baumästen in der Talschlucht bei Tablas, ca. 1800 m, [*Herzog*] *4666*. Types. An Baumästen in der Talschlucht bei Tablas, ca. 1800 m, Mai 1911, leg. *Th. Herzog 4666* (JE, holotype; H, L, S, isotypes).

Pilotrichella allionii Broth., Rev. Bryol. 47: 14. 1920 [1921]. Protologue. [Ecuador] Prov. de l'Oriente. Gualaquiza; in arboribus ad ripam fl. Bomboiza prope ejus confluentiam cum fl. Gualaquiza; 800–900 m [*M. Allioni*]. Gualaquiza; in silva El Salado; 950 m [*M. Allioni*]. Types. Ecuador–Oriente–V. Bomboiza. Ad arborum ramos in silva "El Salado" frequens sed permisita Gualaquiza m 950, 25 Aug. 1910, *M. Allioni 497* (H, lectotype); V. Bomboiza, Ad truncos in sylva El Salado, 950 m, 25 viii 1910, *M. Allioni* (PC, isolectotype); Ecuador, prov. Azuay. Gualaquiza: ad ripam flum. Bomboiza prope ejus confluentiam cum fl. Gualaquiza, in arboribus, Jul. 1909, legit *Rev. M. Allioni* (H, syntype).

Plants slender to medium-sized, dull, light green, yellow green, reddish yellow, or brownish green, in loose mats, often with pendent strands. Stolons yellow to red, creeping; rhizoids consistently on stolons, also at base of stipitate secondary stems, or on flagelliform branch tips, red, not or irregularly branched, from clusters of initials abaxial to the leaf insertions; leaves widely spaced, reduced, erect, ovate-triangular, abruptly acuminate, ecostate, 1.0–1.4 mm long. Stems stipitate or nonstipitate, horizontal, erect or pendent, frequently and irregularly branched, branches at times filliform-attenuate, 4–10(–40) cm long, yellowish green, becoming dark red with age; stems in cross section with sclerodermis of 3–5 small, thick-walled, reddish orange cells, cortical cells enlarged, firm-walled, pale yellow, red with age, central strand absent; paraphyllia and pseudoparaphyllia absent, scale leaves present; axillary hairs 3–4 cells long, basal 1–2 cells quadrate to subquadrate, reddish brown, upper 2–3 cells broadly cylindrical, hyaline or reddish. Stipe leaves ovate, cordate, rounded at base or straight to the insertions. Stem and branch apices turgid; stem and branch leaves differentiated only in size, stem leaves not or obscurely seriately ranked when dry, branch leaves often distinctly seriately ranked when dry or wet, leaves obovate to oblong-obovate, erect to erect-spreading, variously clasping below, 1.0–1.6 mm long, at times somewhat auriculate, apex cuspidate; margins broadly incurved and sharply serrulate above, plane or broadly incurved, serrulate or entire below; costae mostly absent, occasionally short double or short single; leaf cells long-flexuose, smooth, upper cells 20–30 × 4–6 μm, median cells 30–60 × 3–4 μm, outer basal cells shorter and broader, inner basal cells near insertions elongate, often porose; alar cells red to red yellow, subquadrate to short-rectangular, extending up the margins in 2–4 rows and across the insertion in 4–6 rows, yellow across the insertions. Dioicous. Perigonia gemmiform, lateral on secondary stems and branches. Perichaetia lateral; leaves lanceolate, vaginulae moderately hairy. Setae short, wavy, 2.5–7.0 mm long, smooth below, roughened above, yellow, becoming yellowish red with age. Capsules exserted, erect to somewhat inclined, ovoid to short-cylindrical, 1.0–2.0 mm long, neck moderately developed; exothecial cells

small, rounded in 2–3 rows below the mouth, subquadrate, irregularly short-rectangular, or oblate, firm-walled below, cells in neck smaller than the median cells; stomata superficial on neck; opercula obliquely long-rostrate, 1.0–1.5 mm long; annuli rudimentary, of 2–3 rows of thin-walled enlarged cells; peristome yellowish white; exostome teeth linear, to 0.5 mm long, dorsal (outer) surface lightly horizontally striate at base, smooth or finely papillose above, trabeculae weakly developed on both sides; endostome nearly as long as exostome, basal membranes very low, segments filamentous, narrowly perforate, not keeled, smooth to papillose, cilia rudimentary or absent. Spores round, lightly roughened, 14–20 μm long. Calyptrae 2–3 mm long, narrowly cucullate, smooth to lightly hairy.

Illustrations. Herzog (1916, Fig. 41 a–b); Bartram (1949, Fig. 118 A–C, as *Pilotrichella rigida*); Florschütz (1964, Fig. 100); Churchill (1994, Fig. 27 C, as *Pilotrichella pentasticha*); Sharp *et al.* (1994, Fig. 537, as *Pilotrichella rigida*); Churchill and Linares (1995, Fig. 124 a–g, as *Pilotrichella pentasticha*); Buck (1998, Pl. 91 9–17, as *Orthostichella pentasticha*); Gradstein *et al.* (2001, Fig. 156 A–I, as *Orthostichella pentasticha*); Buck (2003, Fig. 126); Allen and Magill (2007, Fig. 9). Figure 100.

Habitat. On tree trunks, branches, and twigs, vines, shrubs, logs, leaves, and tree fern fronds, occasionally on moist rocks along rivers and boulders along roadsides and dry slopes; 50–2600 m.

Distribution in Central America. BELIZE. Cayo: *Allen 18428* (BRM, MO); Toledo: *Allen 18746* (BRM, MO). GUATEMALA. Alta Verapaz: *Steyermark 44571* (F, FH, MO); Izabal: *Steyermark 39991* (FH, MO); Petén: *Morgan 16* (MO); San Marcos: *Standley 85522* (F, FH, MO); Suchitepéquez: *Steyermark 46666* (F, FH, MO, US). EL SALVADOR. Ahuachapán: *Davidse et al. 37473A* (MO). HONDURAS. Atlántida: *Allen 17467* (MO); Lempira: *Allen 12148* (MO); Olancho: *Allen 12777B* (MO); Santa Bárbara: *Crosby 2793* (MO); Yoro: *Allen 13664* (MO). NICARAGUA. Estelí: *Moreno 19249* (H, MO, NY, S, US); Jinotega: *Stevens 16695* (HNMN, MO); Matagalpa: *Stevens 22193* (MO). COSTA RICA. Alajuela: *Standley & Torres 47705* (H); Cartago: *Liesner & Judziewicz 14486* (MO, NY); Guanacaste: *Crosby 3851* (MO, S); Heredia: *Crosby 9938* (MO); Puntarenas: *Dauphin 1983* (MO); San José: *Crosby & Crosby 5774* (CR, MO). PANAMA. Bocas del Toro: *Allen 5844* (MO); Chiriquí: *Croat 15925* (MO); Coclé: *Witherspoon 8771* (MO); Colón: *Crosby 10354* (MO); Darién: *Allen 8697* (MO, PMA); Panamá: *McDaniel 6893* (MO); Veraguas: *Knapp & Sytsma 2543* (BM, H, MO, NY, PMA, S, US).

World range: Mexico; Central America; Caribbean; Western, Northern, and Southern South America, Brazil; West and East Tropical Africa; Western Indian Ocean.

Orthostichella versicolor is the most commonly occurring species of the genus in Central America. It has creeping stolons and erect or pendent (at times hanging 1.0–1.5 m) stems that can be strongly stipitate or nonstipitate. Single stolons at times have both types of stems. The branches often end in filiform attenuations or become transformed into stolons. Although the stolons, stems, and branches can be morphologically distinct and abruptly transformed from one into another, more often they intergrade with each other. Spirally ranked branch leaves (and occasionally stem leaves) are a typical feature of *O. versicolor*. The leaves in *O. versicolor* are usually cuspidate, have distinctive incurved, serrulate upper leaf margins, elongate, smooth, firm-walled leaf cells, and weakly developed, reddish yellow, firm-walled alar cells that usually reach the outer, basal margins. The leaf costae in *O. versicolor* are wildly variable in expression; most leaves are ecostate, but here and there leaves can be found with short double, short single, or long single costae. Sporophytes are not often found in this dioicous moss. The setae are 2–6 mm long, flexuose, and roughened above. The opercula are long, obliquely rostrate, and the peristome is pale yellow and greatly reduced. Distinctive features of the peristome include its narrow, mostly papillose exostome teeth that are weakly cross-striate at the very base and narrow endostomial segments that are perforate but not keeled. The calyptrae are cucullate and either naked or variously hairy. *Orthostichella versicolor* is primarily an epiphytic species that occasionally is found on boulders. When growing on twigs the species has small plants with weakly ranked leaves, while plants on tree trunks are often robust and have strongly ranked leaves.

There are two major forms of *O. versicolor*. The typical form, nomenclaturally centered on *O. versicolor*, has non-stipitate stems, strongly ranked branch leaves that are straight at the insertions, and alar cells that usually reach the basal margin. The second form, nomenclaturally centered on *Neckera pachygaster*, has somewhat turgid plants that are distinctly stipitate and have weakly ranked

leaves. The stem leaves are auriculate, and the branch leaves are straight or rounded to the insertions. When the branch leaves are rounded to the insertions, the alar cells usually do not reach the basal leaf margins. This form of the species is very close to *O. rigida*, and some collections, especially from Africa where *O. rigida* is more variable, are nearly impossible to place. Throughout the range of *O. versicolor*, there are slender expressions that lack stipitate secondary stems and have more or less unranked branch leaves that are straight to the insertions. *Orthostichella rigida* differs from *O. versicolor* in having clasping branch leaves that are appressed rather than erect and rounded to auriculate at base, with alar cells that do not reach the outer margins of the leaves. Although many collections of *O. versicolor* exhibit one or another of its distinctive forms, there are some especially large collections that display every one of the morphological expressions of the species.

Orthostichella versicolor can be confused with *O. pachygastrella*, the most commonly occurring species of *Orthostichella* in southern South America, or *O. welwitschii* (Duby) B. H. Allen & Magill, which is present in northern South America. *Orthostichella pachygastrella* is a slender species that may or may not have stipitate stems, and it has distinctly ranked branch leaves. It differs from *O. versicolor* in having auriculate secondary stem and branch leaves, and deciduous branch leaves. *Orthostichella welwitschii* is extremely close to the typical expression of *O. versicolor* in size, leaf stance, and in having branch leaves straight to the insertions. It differs from *O. versicolor* in having abruptly long hair-pointed stolon and primary stem leaves.

In the field, *Orthostichella versicolor* can be confused with *Squamidium nigricans*, *Orthostichopsis tenuis* (A. Jaeger) Broth., *Orthostichopsis praetermissa* W. R. Buck, or *Orthostichidium quadrangulare*, because they all are pendent mosses with distinctly ranked leaves. The first three species differ from *Orthostichella versicolor* in having a long single costa. *Squamidium nigricans* also has well-developed alar cells and often a black coloration, while the two *Orthostichopsis* species have filamentous pseudoparaphyllia, densely hairy calyptrae and vaginulae, and cylindrical capsules. *Orthostichopsis praetermissa* further differs from *Orthostichella versicolor* in having hair-pointed leaves.

Orthostichidium quadrangulare is especially close to *Orthostichella versicolor*, since both species have ecostate leaves with broadly incurved upper leaf margins and weakly developed alar cells. Plants of *Orthostichidium quadrangulare* tend to be a little larger than those of *Orthostichella versicolor*, and its leaves are more stiffly erect as well as more strongly ranked. However, the only certain way to separate *Orthostichidium quadrangulare* from *Orthostichella versicolor* is to examine their branch primordia. In *Orthostichidium quadrangulare*, the primordia often give rise to clusters of uniseriate gemmae and they are surrounded by filamentous pseudoparaphyllia. *Orthostichella versicolor* never has asexual gemmae, and the branch primordia are surrounded by scale leaves.

Orthostichella versicolor has generally been known in Central America as *Pilotrichella pentasticha* (Brid.) Wijk & Margad. or *Orthostichella pentasticha* (Brid.) W. R. Buck, because Robinson (1967) treated the species in Colombia. The type collection of *Hypnum pentastichum* (in PC) was made by Philibert Commerson on Mauritius in 1769 or 1770; it belongs to the genus *Orthostichidium*.

7. *Pinnatella* M. Fleisch., Hedwigia 45: 79. 1906.

Hypnum Hedw. sect. *Pinnatella* Müll. Hal., Linnaea 39: 456. 1875, invalid name, lacks a description.
Porotrichum (Brid.) Hampe sect. *Pinnatella* Müll. Hal., Linnaea 40: 272. 1876, invalid name, lacks a description.

Plants small, medium-sized, or robust (outside Central America), stipitate-frondose, somewhat flattened, forming dark green to sordid green or yellowish green, lax tufts. Stolons creeping; rhizoids smooth, reddish brown, not or sparsely branched, in circular clusters just below the leaf insertions, on stolons, and at the base of stipitate stems; leaves loosely imbricate, widely spaced, evenly foliate, triangular-lanceolate. Stems erect, stipitate, irregularly pinnate to bipinnate, complanate-foliate, at times flagellate-attenuate; stems in cross section with sclerodermis of small, thick-walled cells, grading into somewhat larger, firm- to thick-walled cortical cells, central strand present or absent (outside Central America); paraphyllia absent; pseudoparaphyllia absent or sparsely present. Stipe leaves erect-spreading to spreading from a somewhat clasping, decurrent base, evenly foliate, triangular-lanceolate to ovate-triangular, acute to acuminate; margins entire to subserrulate, narrowly recurved to above midleaf; costae single, ending below apex. Stem leaves erect-spreading, strongly flattened,

imbricate, somewhat plicate when dry, oblong-ligulate to oblong-ovate, more or less symmetric or asymmetric (outside Central America), broadly acute, rounded, or obtuse, sometimes apiculate or mucronate, shortly decurrent; margins usually shortly incurved below on one side, occasionally plane throughout, crenulate to serrulate above, crenulate to subentire below; costae single, strong, ending near the apex, or occasionally double or deeply bifurcate (outside Central America), often sinuose, forked above, and spurred below; cells smooth or prorate, upper cells isodiametric, irregularly rounded, rounded-hexagonal, or subrhomboidal; basal cells rectangular, oblong, or elongate; alar cells oblate, quadrate, or short-rectangular in several rows at the basal angles, at times poorly developed; intramarginal limbidia of 1–several rows of somewhat elongate cells in lower 1/2 of leaf variously developed. Branch leaves erect to erect-spreading, weakly flattened, at times incurved when dry, oblong-ovate, smaller than the stem leaves but otherwise similar. Asexual reproduction by axillary, microphyllous, flagelliform branches. Dioicous. Setae elongate, smooth below, roughened above, rarely smooth throughout. Capsules erect, symmetric, cylindrical; stomata on neck, rarely absent; opercula obliquely conic-rostrate; peristome diplolepideous; exostome teeth narrowly triangular, dorsal surface spiculose-papillose throughout, trabeculae weakly developed, not projecting; endostome as long as exostome teeth, basal membranes high, segments narrowly lance-subulate, spiculose-papillose throughout, narrowly perforate, cilia absent or rudimentary. Calyptrae without distinct slits (campanulate?), hairy (with paraphyses), smooth.

Pinnatella is a pantropical genus of 15 species. The center of diversity of the genus is in southern and southeastern Asia. The genus was revised by Enroth (1994a), who characterized it as having spreading to squarrose stipe leaves with recurved margins, small, single-celled teeth on the apical leaf margins, a strong costa ending near the apex, leaves with short marginal cells and an intramarginal limbidium of elongate cells, roughened setae, and a reduced, neckeroid-type peristome. Enroth (1994a) considered the genus critical in understanding the relationship between the Thamnobryaceae and Neckeraceae, because it had a thamnobryoid gametophyte, but a neckeroid sporophyte.

The single Central American species of *Pinnatella* is also the most broadly distributed and the only one present in the Neotropics and Africa. Since its sporophytes are not known in the Neotropics, only gametophytic features can be used to recognize it there. In Central America the genus could be confused with *Homaliodendron*, *Porotrichum*, or *Thamnobryum*. *Homaliodendron* differs from the Neotropical species of *Pinnatella* in lacking a stem central strand and in having closely appressed, plane-margined stipe leaves. Its leaves are more asymmetric that those of *Pinnatella*, they have shorter, weaker costae, and they lack an intramarginal limbidium of elongate cells. Most Neotropical species of *Porotrichum* are considerably larger than those of *Pinnatella*, and they have more asymmetric leaves, with typically weaker costae that taper and sometimes are toothed below or end in a spine. In addition, *Porotrichum* leaves usually have fusiform to elongate median leaf cells and large teeth on the apical margins; they lack an intramarginal limbidium of elongate cells. In technical terms, there is little distinction between the gametophytes of *Thamnobryum* and *Pinnatella*, while sporophytically *Thamnobryum* differs from *Pinnatella* primarily in having an unreduced hypnoid peristome. In practical terms, however, Central American *Thamnobryum* species are considerably larger than those of *Pinnatella*; they have more sharply serrate apical leaf margins and scale-like, appressed stipe leaves with plane leaf margins. According to Enroth (1994a), there are some species of *Thamnobryum* that have an intramarginal limbidium of elongate cells similar to that seen in *Pinnatella.*

The name *Pinnatella* combines the Latin *pinna* (primary division of a compound leaf) with the diminutive *-ella*, and it probably refers to the irregularly pinnate branching of some of its species.

Pinnatella minuta (Mitt.) Broth., Nat. Pflanzenfam. I(3): 857. 1906. *Porotrichum minutum* Mitt., J. Linn. Soc., Bot. 12: 465. 1869. Protologue. Ins. Cuba, *Wright*, inter n. 85.

Porotrichum paraguayense Broth., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 26 Afd. 3(7): 42. 1900. *Pinnatella paraguayensis* (Broth.) Broth. *ex* Paris, Coll. Nom. Broth. 24. 1909. Protologue. Paraguay: Pirapó, ad arbores silvarum [*Lindman*] (n. 271).

Pinnatella jamaicensis E. B. Bartram *in* Orcutt, Jamaica Naturalist 1: 17. 1928. Protologue. Balaclava Jamaica, August 5, 1927, *C. R. Orcutt No. 2352e.*

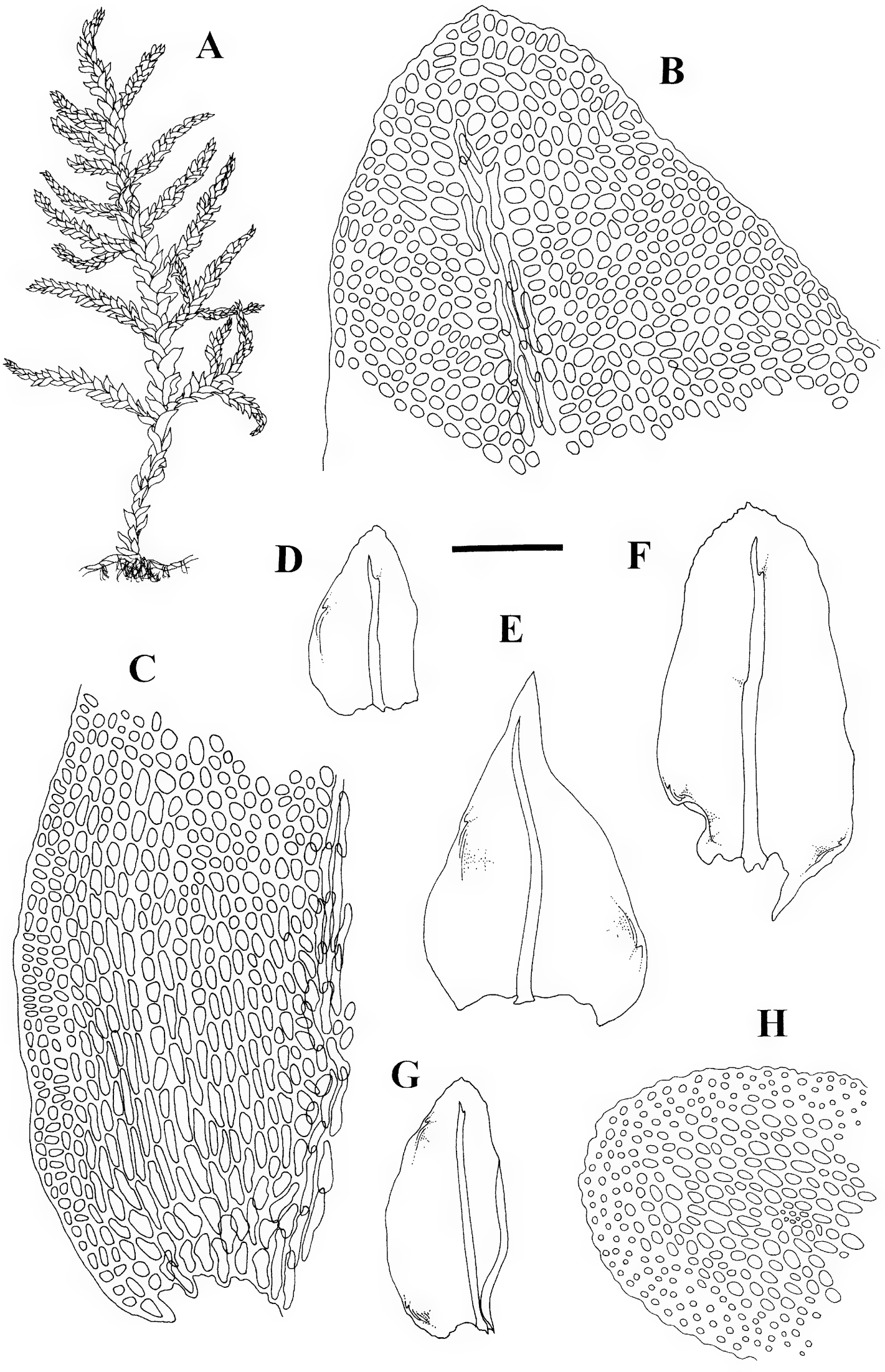


Figure 101. *Pinnatella minuta*. A. Habit. B. Leaf apex. C. Basal and alar cells. D & G. Branch leaves. E. Stipe leaf. F. Stem leaf. H. Stem in cross section. Scale in mm: bar = 0.05 (B, C); bar = 0.06 (H); bar = 0.2 (D–G); bar = 2.5 (A). All figure parts from *Allen 18045*.

Plants small to medium-sized, 10–30 mm high, stipitate-frondose, somewhat flattened, forming dark green to sordid green or yellowish green, lax tufts. Stolons creeping; rhizoids smooth, reddish brown, not or sparsely branched, in circular clusters just below the leaf insertions, on stolons, and at the base of stipitate stems; leaves loosely imbricate, widely spaced, evenly foliate, triangular-lanceolate. Stems erect, stipitate, irregularly pinnate to bipinnate, complanate-foliate, at times flagellate-attenuate; stems in cross section with sclerodermis of 3–7 rows of small, thick-walled cells, grading into somewhat larger, firm- to thick-walled cortical cells, central strand poorly developed; paraphyllia absent; pseudoparaphyllia foliose, subfoliose, or absent. Stipe leaves erect-spreading to spreading from a somewhat clasping, decurrent base, evenly foliate, triangular-lanceolate to ovate-triangular, 0.7–1.0 mm long, acute to acuminate; margins entire to subserrulate, narrowly recurved to above midleaf; costae single, ending below apex. Stem leaves 0.7–1.3 mm long, erect-spreading, variously flattened, imbricate, somewhat plicate when dry, oblong-ligulate to oblong-ovate, more or less symmetric, broadly acute, rounded, or obtuse, sometimes apiculate or mucronate, shortly decurrent; margins crenulate to serrulate above, crenulate to subentire below, usually shortly incurved below on one side, occasionally plane throughout; costae single, strong, ending near the apex, often sinuose, forked above, and spurred below; cells smooth or prorate, upper cells isodiametric, irregularly rounded, rounded-hexagonal, or subrhomboid, 7–10 µm; basal cells rectangular, oblong, or elongate, 20–40 µm long; alar cells oblate, quadrate, or short-rectangular in several rows at the basal angles, at times poorly developed; intramarginal limbidium of 1–2 rows of somewhat elongate cells in lower 1/2 of leaf variously developed. Branch leaves erect to erect-spreading, weakly complanate, at times incurved when dry, oblong-ovate, smaller than the stem leaves but otherwise similar. Asexual reproduction by axillary, microphyllous, flagelliform branches. Dioicous. Sporophytes unknown in the Neotropics, description from Enroth (1994a). Perichaetia leaves to 1.1 mm long, ovate at base, short and broadly lanceolate above, apex acute, occasionally obtuse; margins entire below, denticulate above; costae single ending below leaf apex. Setae 2–3 mm long, smooth below and mammillose above, reddish yellow. Capsules erect, symmetric, cylindrical, 1.3–1.7 mm long; median exothecial cells more or less isodiametric near mouth, irregularly rectangular, pentagonal, hexagonal, or subquadrate, somewhat thin-walled below; stomata on neck; opercula obliquely conic-rostrate; peristome diplolepideous; exostome teeth lanceolate, 0.45 mm long, dorsal surface spiculose-papillose throughout, trabeculae weakly developed, not projecting; endostome as long as exostome teeth, basal membranes 80 µm high, segments narrowly lance-subulate, spiculose-papillose throughout, narrowly perforate, cilia absent. Spores 12–15 µm, faintly papillose. Calyptrae without distinct slits (campanulate?), hairy (with paraphyses), smooth.

Illustrations. Duby (1871, Pl. 3 4, as *Hypnum africanum*; Pl. 4 7, as *Thuidium filiferum*); Renauld and Cardot (1899, Pl. 87 2, as *Porotrichum chenagonii*); Potier de la Varde (1925, Fig. 11, as *Pinnatella letestui*); Bartram (1928b, Fig. 1 G–I, as *Pinnatella jamaicensis*); Potier de la Varde (1936, Fig. 42, as *Pinnatella letestui*); Bartram (1949, Fig. 127 A–C); Gangulee (1976, Fig. 711, as *Pinnatella africana*); Enroth (1994a, Figs. 2 d, 13); Sharp *et al.* (1994, Fig. 563); Duarte Bello (1997, Pl. 214); Buck (1998, Pl. 44); Magill and Rooy (1998, Fig. 165 1–8); Gradstein *et al.* (2001, Fig. 216 E–H). Figure 101.

Habitat. On rocks; 80–1675 m.

Distribution in Central America. BELIZE. Cayo: *Allen 18045* (MO). GUATEMALA. Baja Verapaz: *Sharp 2856* (FH, MO); Petén: *Lundell 2930* (FH, MO). COSTA RICA. Guanacaste: *Dauphin et al. 2577* (MO); Limón: *Gutierrez* (FH).

World range: Mexico; Central America; Caribbean; Western and Southern South America, Brazil; West, West-Central, East, and South Tropical Africa, Southern Africa, Western Indian Ocean; Indian Subcontinent.

In Central America *Pinnatella minuta* is a small moss with secondary stems reaching only 3 cm high; however, in Africa it can be fairly robust with plants sometimes 10 cm high (Enroth 1994a). Plants of *P. minuta* have a complex morphology, with creeping stolons and erect, stipitate stems that are irregularly pinnately to bipinnately branched. Its secondary stems and branches often end in filiform attenuations, and the species appears to reproduce asexually by microphyllous, flagelliform branches that arise in its leaf axils. The stems, and to a lesser degree branches, of *P. minuta* are com-

planate, with more or less symmetric, oblong-ligulate to oblong-ovate leaves that vary from broadly acute to obtuse. The leaf margins are typically incurved below on one side and crenulate to serrulate above. Its costae are single, strongly developed, ending near the apex, sinuose and often spurred below, and at times forked above. Its upper leaf cells are predominantly isodiametric, oval or rounded-rhomboid, thick-walled, and they can be smooth or prorate. At base, especially near the costa, the cells are more or less elongate, and the alar cells consist of only a few isodiametric to oblong-rectangular cells. The outstanding leaf feature of *P. minuta* is the presence in the lower half of the leaf of an intramarginal border of cells that are distinctly longer than the surrounding cells.

Homaliodendron piniforme, *Porotrichum brevifolium*, and *Porotrichum substriatum* are somewhat similar to *P. minuta* in size. They differ from *P. minuta* in having more asymmetric stem and branch leaves that often have serrate leaf margins and weaker costae that reach only 1/2–2/3 the leaf length and taper at the ends; another distinction is an intramarginal limbidium in the leaves. *Homaliodendron piniforme* also differs from *P. minuta* in lacking a stem central strand, while the *Porotrichum* species further differ in having fusiform to elongate median leaf cells.

8. *Porotrichodendron* M. Fleisch., Musci Buitenzorg 3: 937. 1908.

By Robert R. Ireland & Bruce Allen

Plants medium-sized to robust, 3–20 cm long or 1.5–5.5 cm tall, yellowish green to light green, glossy. Primary stems creeping; secondary stems scattered along primary stems ascending to erect, irregularly pinnate to bipinnate, from a stipitate base, complanate to somewhat terete-foliate, usually ending in a cuspidate tip; secondary stems in cross section with sclerodermis of 5–9 rows of small, thick-walled cells, cortical cells enlarged, somewhat thick-walled, central strand present, weakly differentiated, or absent; pseudoparaphyllia on secondary stems and branches, foliose when mature, sometimes a few undeveloped filamentous ones intermixed, linear-lanceolate, lanceolate to broadly ovate, a few teeth or serrations often on margins; axillary hairs 3–5 cells long, basal 1–2 cells short, upper 2–4 cells elongate; branches of secondary stems with sclerodermis of 4–6 rows of thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; flagellate branchlets sometimes present. Stipe leaves scarious, ovate-lanceolate, often with a narrow apex, appressed to somewhat spreading. Stem leaves mainly complanate to somewhat moderately concave, occasionally somewhat undulate, erect-spreading, oblong-lanceolate to oblong-ovate, broadly acute to nearly obtuse, often abruptly cuspidate to acuminate, sometimes weakly auriculate at base, often orange to slightly reddish across insertion; margins sometimes irregularly serrate with multicellular serrations near apex, serrate to serrulate in upper half, sometimes nearly entire, plane or incurved above; costae single, narrow, extending 2/3–3/4 the leaf length, sometimes ending in a small spine on the dorsal surface; cells smooth, rhombic near apex, linear to linear-rhomboidal below, thin- to thick-walled, often porose toward insertion, usually thick-walled at apex; alar cells often shorter and broader, sometimes orange to slightly reddish. Branch leaves concave, smaller than stem leaves, smooth or sometimes finely striate, erect-spreading, oblong-lanceolate to oblong-ovate, gradually acuminate to abruptly acute, often orange across the insertion; margins irregularly serrate to serrulate in upper half, often nearly to base, mostly incurved above, rarely plane; costae single, narrow, extending 1/2–2/3 the leaf length, sometimes weak and short to nearly lacking; cells smooth, rhombic near apex, linear to linear-rhomboidal below, often thick-walled, frequently porose nearly to apex; alar cells shorter and somewhat broader, occasionally orange to slightly reddish. Asexual reproduction at times by small, deciduous leaves on slender branchlets in leaf axils near tips of branches. Dioicous. Perigonia lateral, scattered mostly along upper parts of stems; leaves short, ovate-acuminate. Perichaetia lateral, scattered along upper parts of stems; leaves large, ovate-lanceolate, with short to long, subulate-spreading apices. Setae solitary, reddish, smooth, elongate, erect to somewhat flexuose. Capsules erect and symmetric or inclined, ovoid to oblong-cylindric, smooth; opercula obliquely long-rostrate, arcuate, as long or longer than capsule; annuli large, persistent; peristome diplolepideous; exostome teeth light brown, long, slender, cross-striolate at base, papillose above; endostome as long as exostome, white, densely papillose, basal membranes high, segments slender, keeled, perforate, cilia 1–2, rudimentary, or none. Calyptrae cucullate, extending to capsule mouth, naked.

Porotrichodendron is a genus of three species found in the West Indies, Mexico, Central America, and South America. There is a single record of the genus from the Philippines collected in 1870, but it has never been re-collected there. The Philippine collection was made by Gustav Wallis (1830–1878), who spent the last eight years of his life collecting in the Philippines and Japan (1870–1871), North America (1871–1872), and Colombia, Panama, and Ecuador (1872–1878). Müller (1874) treated the Wallis Philippine and Colombian mosses in the same paper, and since the Philippine collection is identical to the common Neotropical species of *Porotrichodendron*, it seems likely the collection was mislabeled.

Fleischer (1908) originally placed *Porotrichodendron* in the Lembophyllaceae. He considered it to have the habit of many *Porothamnium* species, and placed it close to *Dolichomitra* Broth. The Lembophyllaceae as constituted by Brotherus (1906a, 1907b, 1925) and Fleischer (1908) represented an odd assortment of genera with very little similarity. Crum (1991), in contrast, considered only stipitate plants with concave leaves and well-differentiated, small, thick-walled alar cells to characterize the family. *Porotrichodendron* was transferred to the Neckeraceae by Buck (1998) on the basis of its stipitate-frondose habit and coarsely serrate leaf apices. Within the Neckeraceae, the genus is most similar to the thamnioid genera, with which it shares a stipitate-frondose habit, leaves with strong single costae and weakly developed alar cells, elongate setae, and exostome teeth that are cross-striate at base. Plants of *Porotrichodendron* can be evenly foliate or have complanate-foliate stems. These latter plants closely approach *Porotrichum*. In an absolute sense, *Porotrichodendron* differs from *Porotrichum* only in having leaves that are rounded to somewhat auriculate at base.

The name *Porotrichodendron* combines the generic name *Porotrichum* with the Greek noun *dendron* (tree).

1. Stem leaves concave; branch leaves smooth, ovate to oblong-ovate, very concave, cuspidate, cuspid erect to slightly recurved; apical leaf cells 8–14 × 4–8 µm . . . . . 2. *P. lindigii*
1. Stem leaves complanate to slightly concave; branch leaves smooth or striate, lanceolate, oblong-lanceolate or ovate-lanceolate, moderately concave, cuspidate or apiculate; apical leaf cells 12–28 × 2–6 µm 2
2. Stem leaves serrate (serrations 1-celled) or serrulate; margins somewhat inrolled at apices; branch leaves striate, lanceolate to oblong-lanceolate, often cuspidate; apical leaf cells 14–20 × 4–5 µm . . . . . 1. *P. bertrandii*
2. Stem leaves strongly serrate (serrations often 2-celled); margins plane at apices; branch leaves smooth, ovate-lanceolate to oblong-lanceolate, often apiculate; apical leaf cells 12–28 × 2–6 µm . . . . . 3. *P. superbum*

1. *Porotrichodendron bertrandii* (Renauld & Cardot) Broth., Nat. Pflanzenfam. (ed. 2) 11: 206. 1925. *Porotrichum bertrandii* Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 29(1) 181. 1890. Protologue. Haïti, Port-au-Prince, ad truncos arborum (*Bertrand*). Types. Haiti, Port-au-Prince, *Bertrand s.n.* (PC, holotype; BM, H, isotypes).

Plants small to large, creeping, to 15 cm long, or erect and dendroid, 2–5 cm tall, 1–2 cm wide, yellowish, light green to brownish green, glossy. Stems creeping to erect from stolons, stipitate, regular to irregularly pinnate to bipinnate, loosely foliate, usually ending in a broad or rarely cuspidate tip; flagellate branchlets sometimes present. Pseudoparaphyllia foliose, narrowly to broadly ovate, margins serrulate. Stipe leaves appressed, scarious, tips recurved. Stem leaves erect to somewhat spreading, variously striate, slightly concave, oblong-lanceolate, 1.5–2.0 × 0.5–0.8 mm, often cuspidate; margins serrate to serrulate above, serrulate to entire below, incurved in upper half or below; costae extending 1/2–2/3 the leaf length; cells smooth, rhombic near apex, 10–20 × 4–6 µm, linear-fusiform below, 16–36 × 4–6 µm, thick-walled throughout, porose toward the insertion; alar cells weakly differentiated, quadrate to rectangular, hyaline to yellowish, adjacent cells yellowish across base. Branch leaves erect to erect-spreading, often finely striate, concave, lanceolate to oblong-lanceolate, 1.0–1.4 × 0.3–0.4 mm, gradually acute; margins serrate to serrulate at apex, weakly serrulate to entire below, slightly incurved above; costae extending 1/2–2/3 the leaf length; cells smooth, rhombic near apex, 14–20 × 4–5 µm, linear-fusiform below, 22–44 × 3–4 µm wide, thick-walled throughout; alar cells weakly developed, rectangular to quadrate or nearly rounded, hyaline to yellowish, adjacent

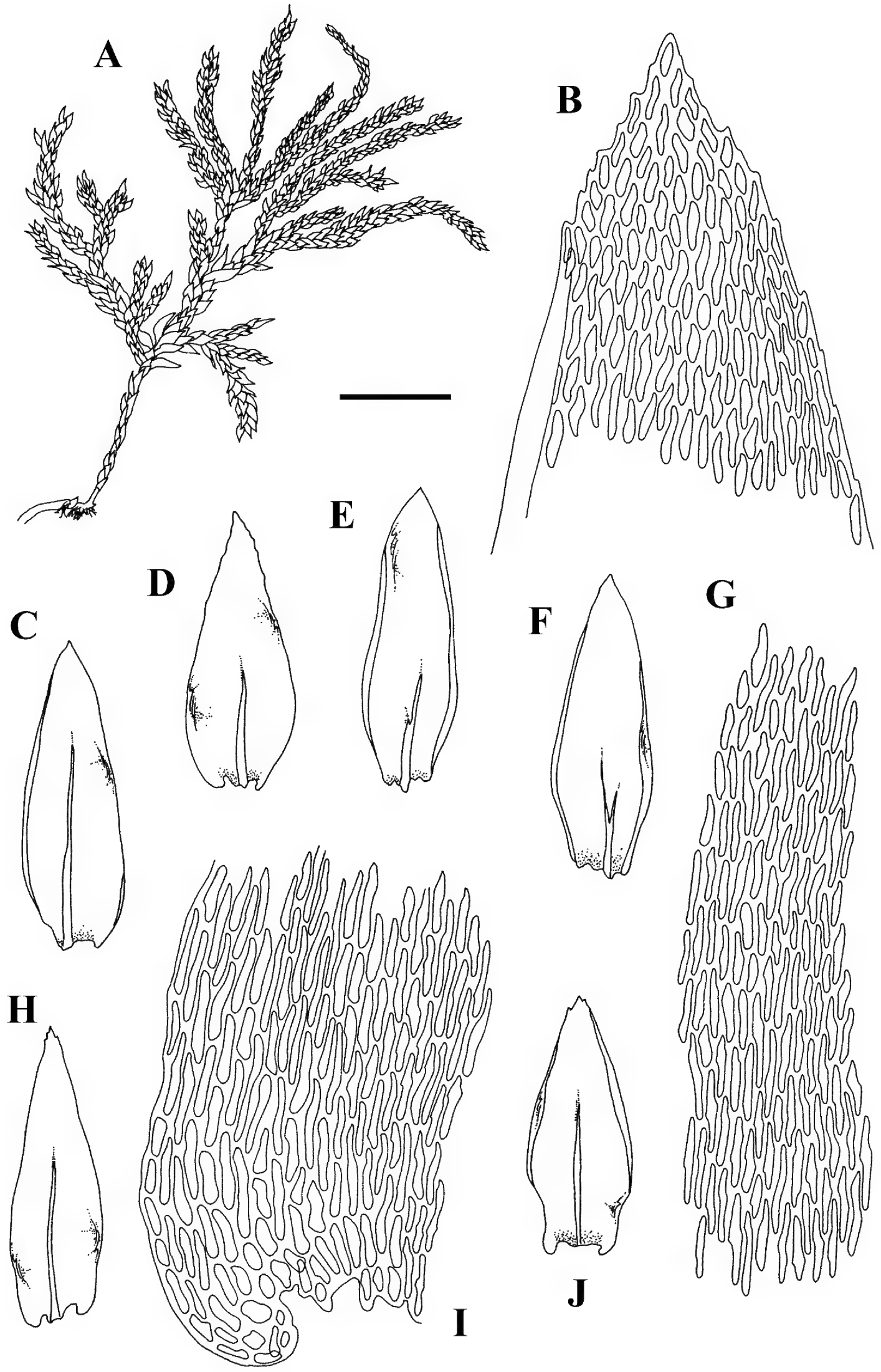
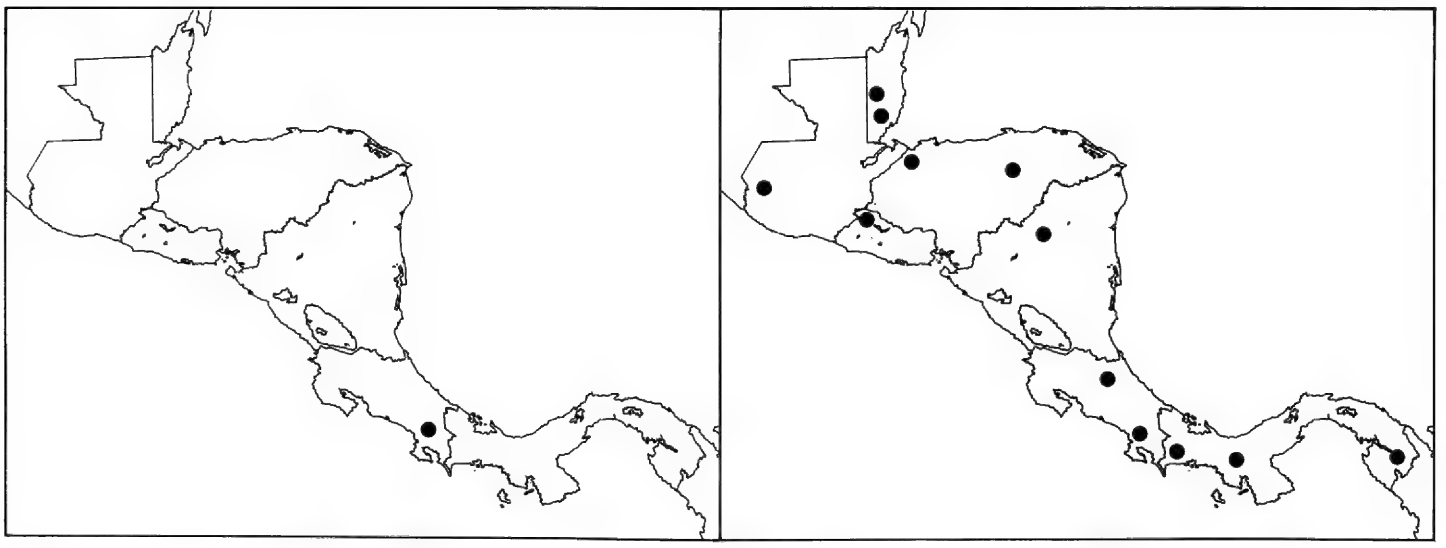


Figure 102. *Porotrichodendron bertrandii*. A. Habit. B. Leaf apex. C–F, H, J. Secondary stem and branch leaves. G. Median leaf cells. I. Basal and alar cells. Scale in mm: bar = 0.05 (B, G, I); bar = 0.4 (C–F, H, J); bar = 4.0 (A). All figure parts from *Bertrand* (type).



Porotrichodendron bertrandii *Porotrichodendron lindigii*

cells yellowish across leaf insertion. Setae flexuose, 1.5–2.5 cm long. Capsules erect to inclined, cylindric, 1.5–2.0 mm long; opercula to 2 mm long.

Illustration. Figure 102.

Habitat. On tree trunks, bases of trees, branches, rotting logs and stumps, vines, humus, and, rarely, limestone rocks in moist forests; 1000–3520 m.

Distribution in Central America. COSTA RICA. Puntarenas: *Spellman et al. B123c* (MO).

World range: Central America; Caribbean; Western and Southern South America.

Porotrichodendron bertrandii is usually a medium-sized species, with distinctly stipitate secondary stems and narrow, slightly concave, more or less plicate stem leaves. Its branch leaves are rounded to the insertions, have serrulate upper margins, and vary from lanceolate to oblong-lanceolate in shape. The branch leaves are gradually acute and sometimes cuspidate and have rhombic to flexuose apical leaf cells.

Porotrichodendron superbum is typically a larger plant than *P. bertrandii* (2–9 cm vs. 2–5 cm high), with weakly stipitate secondary stems. It often has smooth rather than plicate, flattened to complanate stem leaves. The branch leaves of *P. superbum* also differ from those of *P. bertrandii* in being oblong-lanceolate to oblong-ovate, and often apiculate. Furthermore, the apical leaf cells of *P. superbum* are somewhat longer (12–28 µm vs. 14–20 µm) than those of *P. bertrandii*.

Porotrichodendron bertrandii and *P. lindigii* are often similar in size and they both have cuspidate leaf apices. *Porotrichodendron lindigii* differs from *P. bertrandii* in having strongly concave, much broader, ovate to oblong-ovate branch leaves that are smooth when dry, and shorter (8–14 µm vs. 14–20 µm) apical leaf cells.

2. *Porotrichodendron lindigii* (Hampe) W. R. Buck, Mem. New York Bot. Gard. 82: 108. 1998. *Pilotrichum lindigii* Hampe, Ann. Sci. Nat., Bot. sér. 5, 5: 341. 1866. *Porotrichum lindigii* (Hampe) Mitt., J. Linn. Soc., Bot. 12: 461. 1869. Protologue. [Colombia] Bogota, Pacho, in sylvis, 2200 met., inter alia intermixtum legit *A. Lindig*. Type. Colombia, Bogota, Pacho, *Lindig s.n.* (BM, lectotype).

Pirea cavifolia Cardot & Herzog *in* Cardot, Rev. Bryol. 38: 39. 1911. *Pireella cavifolia* (Cardot & Herzog) Cardot, Rev. Bryol. 40: 17. 1913. *Porotrichum cavifolium* (Cardot & Herzog) Magill & B. H. Allen, Novon 2: 123. 1992, illegitimate homonym, not *Porotrichum cavifolium* Broth., 1917. Protologue. [Mexico] État de Vera-Cruz: Mirador (*H. Ross*, 1906; comm. Herzog). État de Hidalgo: Honey-station (Pringle, 1909, *n°15668 in* parte). Types. Mexico, State of Vera-Cruz, Mirador, *H. Ross*, 1906; comm. Herzog (not seen, specimen not in JE); Mexico, State of Hidalgo, Honey-station, *Pringle*, 1909, no. *15668* in part (PC, syntype).

Jaegerinopsis ramosa Thér., Mem. Soc. Cub. Hist. Nat. "Felipe Poey" 14: 358. 1940. Protologue. [Cuba] Sierra Maestra, La Gran Piedra (1100 m); extrait d'une touffe de *Sematophyllum sericifolium* Mitt. (*Ekman 9790 p.p.*).

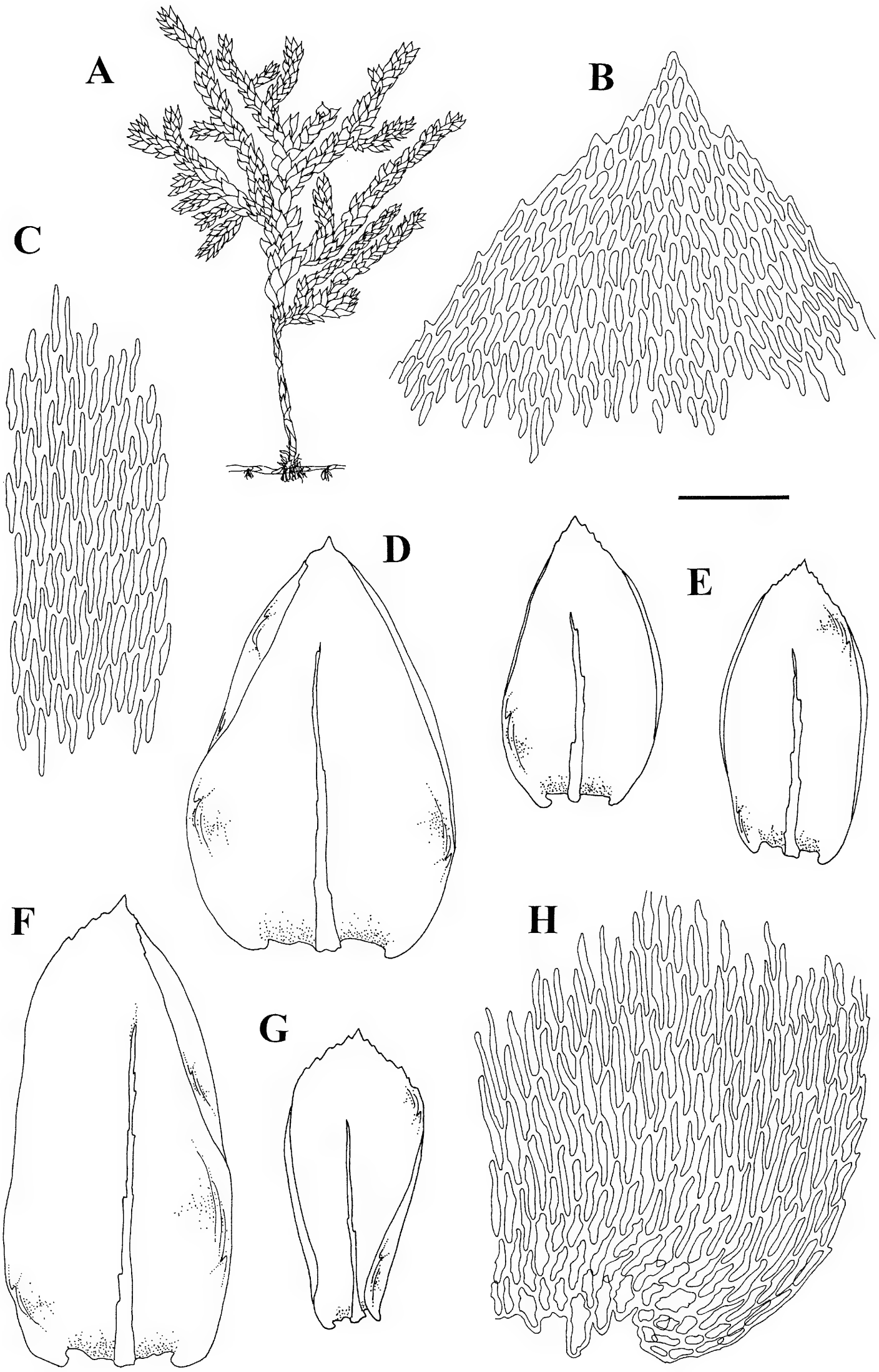


Figure 103. *Porotrichodendron lindigii*. A. Habit. B. Leaf apex. C. Median leaf cells. D & F. Stem leaves. E & G. Branch leaves. H. Basal and alar cells. Scale in mm: bar = 0.06 (B, C, H); bar = 0.4 (D–G); bar = 6.4 (A). D from *Davidse 37201A*; all other figure parts from *Allen 18736*.

Plants small to medium-sized, 1.5–5.5 cm long, yellowish to light green, glossy. Stems ascending to erect from the stolons, stipitate, stems and branches ending in broad to cuspidate tips, regularly to irregularly pinnate or bipinnate; flagellate branchlets sometimes present. Pseudoparaphyllia foliose, narrowly to broadly ovate, margins serrulate. Stipe leaves scarious, appressed to stems. Stem leaves erect, somewhat spreading, concave, broadly ovate, 2.0–2.5 × 1.0–1.5 mm, shortly cuspidate, rounded to the insertions; margins serrulate to nearly entire near apex, entire or sometimes minutely serrulate below, incurved throughout; costae reaching 2/3 the leaf length; cells smooth, thick-walled throughout, porose toward the insertion, apical cells rhombic, 10–16 × 5–8 µm, lower cells long to shortly linear-fusiform, 20–36 × 4–6 µm; alar cells weakly differentiated, of 2–5 short-rectangular cells at the basal angles, cells across the insertions strongly porose, orange. Branch leaves erect-spreading, smooth, strongly concave, ovate to somewhat oblong-ovate, 0.8–1.3 × 0.3–0.6 mm, cuspidate, cusp erect to slightly recurved, weakly rounded to the insertions; margins serrate to serrulate at apex, serrulate to entire below, incurved throughout; costae extending 1/2–2/3 the leaf length, rarely short and double; cells smooth, thick-walled throughout, apical cells rhombic, 8–14 × 4–8 µm, lower cells linear-fusiform, 18–30 × 3–4 µm; alar cells weakly differentiated, of a few short-rectangular cells at the basal angles, cells across the insertions strongly porose, orange. Perigonia, perichaetia, and sporophytes not seen.

Illustrations. Thériot (1940, Pl. 54 5, as *Jaegerinopsis ramosa*); Arzeni (1954, Pls. 22 & 23, as *Pireella cavifolia*); Sharp *et al.* (1994, Fig. 569); Churchill and Linares (1995, Fig. 189 f–k); Duarte Bello (1997, Pl. 188); Buck (1998, Pl. 43 1–7). Figure 103.

Habitat. On tree trunks, fallen trees and branches, rotting logs, rarely on boulders; 725–2000 m.

Distribution in Central America. BELIZE. Cayo: *Allen 15146* (MO); Toledo: *Allen 18736* (BRH, MO). GUATEMALA. San Marcos: *Croat 40961A* (MO). EL SALVADOR. Santa Ana: *Davidse et al. 37203* (MO). HONDURAS. Cortés: *Morton* 7639a (US); Olancho: *Allen 12429* (MO). NICARAGUA. Jinotega: *Standley 10829b* (FH). COSTA RICA. Heredia: *Hatheway & Hatheway 1713* (US); Puntarenas: *Dauphin 1417* (MO). PANAMA. Chiriquí: *Allen 5405* (MO); Darién: *Allen 8917c* (MO); Veraguas: *Croat 34210A* (MO).

World range: Mexico; Central America; Caribbean; Western and Northern South America.

Porotrichodendron lindigii is a small to medium-sized species with distinctly stipitate stems and strongly concave, smooth leaves that often give the plants a tumid appearance. Its branch leaves are rounded to the insertions, typically have serrulate margins, and vary from ovate to somewhat oblong-ovate in shape. The branch leaves are often cuspidate, and have broad rhombic apical leaf cells that give the species a distinctive areolation.

Porotrichodendron superbum is typically a larger plant than *P. lindigii* (2–9 cm vs. 1.5–5 cm high) and it often has flattened to complanate stem leaves. The branch leaves of *P. superbum* and *P. lindigii* are similar in shape. However, those of *P. superbum* are usually apiculate (this feature especially pronounced on the stem leaves) rather than cuspidate. Furthermore, the apical leaf cells of *P. superbum* are longer (12–28 µm vs. 8–14 µm) than those of *P. lindigii* and sigmoid-fusiform in shape.

Porotrichodendron bertrandii and *P. lindigii* are often similar in size and they both have cuspidate leaf apices. The former differs from the latter in having lanceolate to oblong-lanceolate branch leaves that are usually striate when dry and longer (14–20 µm vs. 8–14 µm) apical leaf cells.

The leaves of *Porotrichodendron lindigii* are similar in shape to those of *Porotrichum*. Furthermore, some species of *Porotrichum* and *Porotrichodendron lindigii* have a similar leaf areolation. As a result, *Porotrichodendron lindigii* has been placed in *Porotrichum* (Magill & Allen 1992; Mitten 1869). The Central American species of *Porotrichum* differ from *Porotrichodendron lindigii* in having more or less flattened, complanate leaves that are straight at the insertions, with basal margins often broadly incurved on one side, and better-developed alar cells. *Thamnobryum* and *Porotrichodendron lindigii* are similar in having concave, non-complanate, similarly shaped leaves. *Thamnobryum* differs from *P. lindigii* in having more strongly developed costae and leaves that are straight at the insertions.

3. *Porotrichodendron superbum* (Taylor) Broth. *in* Herzog, Biblioth. Bot. 87: 120. 1916. *Leskea superba* Taylor, London J. Bot. 5: 61.1846. Protologue. [Ecuador] *No. 330*, on trunks of trees, on

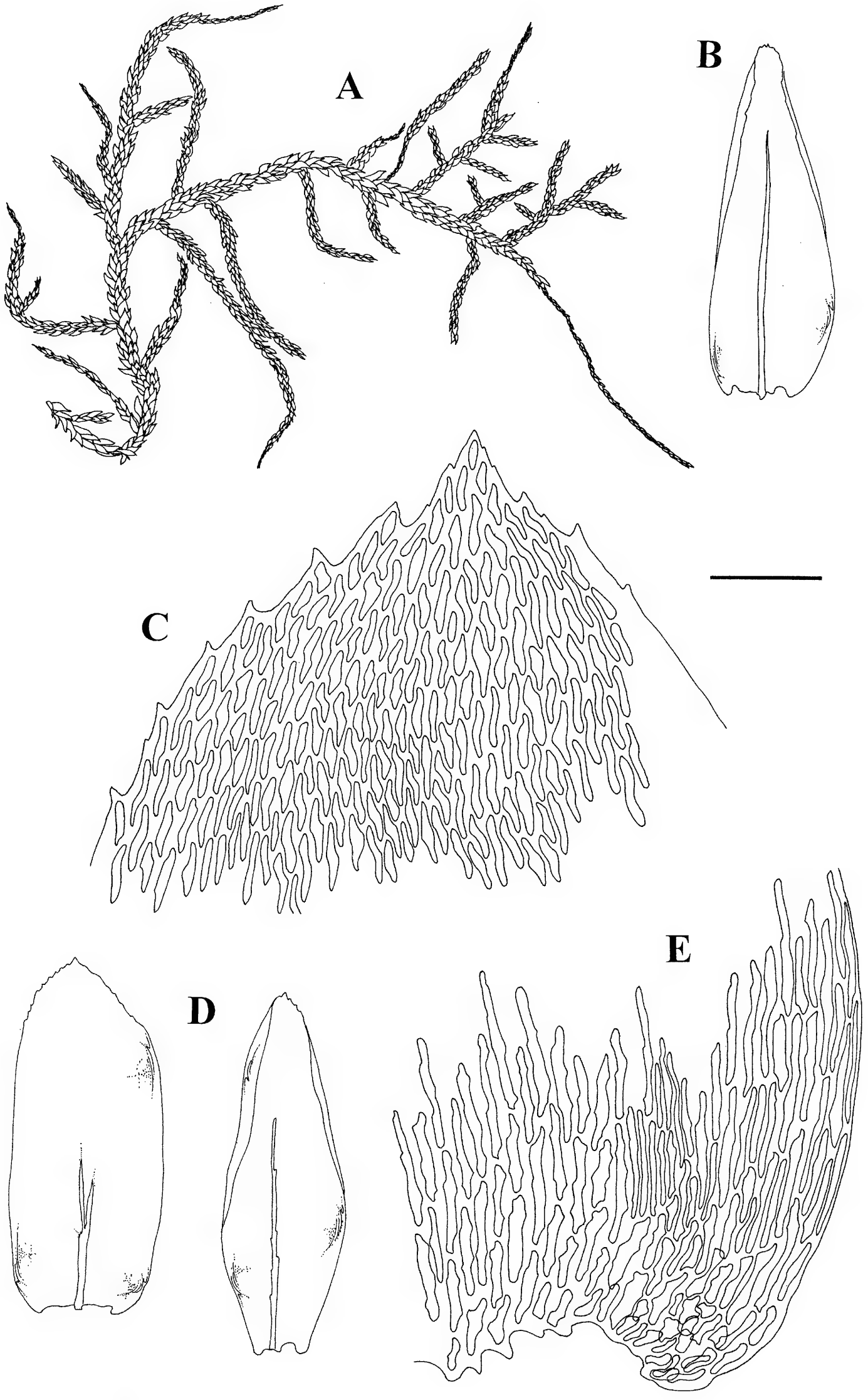
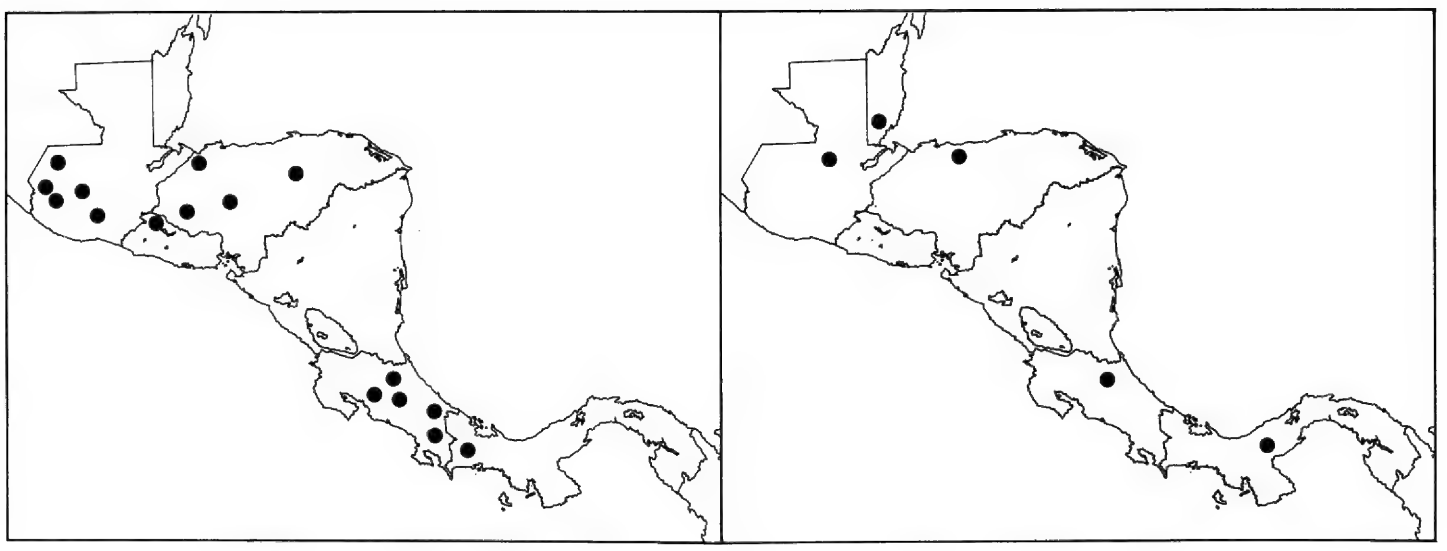


Figure 104. *Porotrichodendron superbum*. A. Habit. B & D. Branch leaves. C. Leaf apex. E. Basal and alar cells. Scale in mm: bar = 0.05 (C, E); bar = 0.5 (B, D); bar = 8.0 (A). All figure parts from *Allen 12062*.



Porotrichodendron superbum *Porotrichum brevifolium*

Pichincha, near Quito, *Prof. William Jameson*, 1845; also, sent collected in 1827 to Dr. R. K. Greville, from the ridge of Pisagua, at an altitude of 10,000 feet, by *Prof. Jameson.* Types. Ecuador, near Quito, *Jameson* in 1845. (FH, lectotype, designated here; BM, isolectotype).

Pilotrichum nitidum Hampe, Ann. Sci. Bot., sér. 5, 5: 340. 1866. *Porotrichodendron nitidum* (Hampe) Broth., Nat. Pflanzenfam. (ed. 2) 11: 206. 1925. Protologue. [Colombia] Hab. Bogotá, Tequendama, 2500 met., in sylvis leg. intermixtam *A. Lindig*. Types. Colombia, Bogotá, Tequendama, *Lindig s.n.* (BM, holotype; H, isotype).

Hypnum mahahaicum Müll. Hal., Linnaea 38: 569. 1874. *Porotrichodendron mahahaicum* (Müll. Hal.) M. Fleisch., Musci Buitenzorg 3: 937. 1908. Protologue. Philippines [?]. Insulae Philippinae, Mahahai, reg. montosa, 6800′ altum: *G. Wallis* 1870. Types. Philippines, Mahahai, *Wallis* s.n. in 1870. (BM, H, isotypes).

Porotrichum filiferum Hampe, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 10: 156. 1874, illegitimate homonym, not *Porotrichum filiferum* Mitt., 1869. *Porotrichodendron filiferum* Broth., Nat. Pflanzenfam. (ed. 2) 11. 206. 1925, new name for *Porotrichum filiferum* Hampe. Protologue. [Brazil] Sub [*A. Glaziou* in vicinia urbis Rio de Janeiro] *Nr 6388*^{b} specimina incompleta more *Neckeracearum* ramis capillaribus degenerantia. Types. Brazil, *Glaziou 6388b* (BM, holotype; H, isotype).

Neckera biformis Hampe, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn ser. 4, 1: 112. 1879. *Porotrichodendron biforme* (Hampe) Broth., Nat. Pflanzenfam. (ed. 2) 11: 206. 1925. Protologue. [Brazil] Inter muscos *Glaziovii* capsi. Type. Brazil, *Glaziou s.n.* (BM, holotype).

Porotrichum substolonaceum Besch. *in* Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32(1): 189. 1894. *Porotrichodendron substolonaceum* (Besch.) Broth., Nat. Pflanzenfam. (ed. 2) 11: 206. 1925. Protologue. [Costa Rica] Bois humides entre la lagune du Barba et le Carrizal, 2800 m (*Pitt.*[*ier*] *n*^{o} *5649*). Montaña de Poás, 2200–2400 m. ([*Pittier*] *n*^{o} *5650*). Fôrets [sic] du Barba ([*Pittier*] *n*^{o} 5651). Types. Costa Rica, entre la lagune du Barba et le Carrizal, 2800 m, *Pittier 5649* (PC, lectotype, designated here; C, H, US, isolectotypes); Montaña de Poás, 2200–2400 m, *Pittier 5650* (PC, syntype); forests of Barba, *Pittier 5651* (PC, syntype).

Porotrichum glaziovii Paris, Index Bryol. 1013. 1898. *Porotrichodendron glaziovii* (Paris) Wijk & Margad., Taxon 10: 26. 1961. Protologue. merid.: Brasil. Austr. or.

Porotrichum flavidulum Müll. Hal., Hedwigia 39: 289. 1900. *Porotrichodendron flavidulum* (Müll. Hal.) Broth., Nat. Pflanzenfam. (ed. 2) 11: 206. 1925. Protologue. Brasilia, Sa. Catharina, Serra Geral, ad truncos arborum araucarieti, Aprili et Majo 1891: *E. Ule, Coll. No. 1144, 1145*. Types. Brazil, Santa Catharina, Serra Geral, *Ule 1145* (H, lectotype, designated here); Brazil, Santa Catharina, Serra Geral, *Ule 1144* (H, syntype).

Porotrichodendron gracile Herzog, Biblioth. Bot. 87: 121. 1916. Protologue. [Bolivia] An der Waldgrenze über Tablas, ca. 3400 m, [*Herzog*] *No. 2875*. Type. Bolivia, *Herzog 2875* (JE, holotype).

Porotrichodendron robustum Broth. *in* Herzog, Biblioth. Bot. 87: 122. 1916. Protologue. [Bolivia] Im Nebelwald über Comarapa, alt. 2600 m, [*Herzog*] *No. 3937.* Types. Bolivia, *Herzog 3937* (H, holotype; JE, PC, isotypes).

Porotrichodendron bolivianum Herzog, Biblioth. Bot. 87: 120. 1916, invalid name, listed in synonymy.

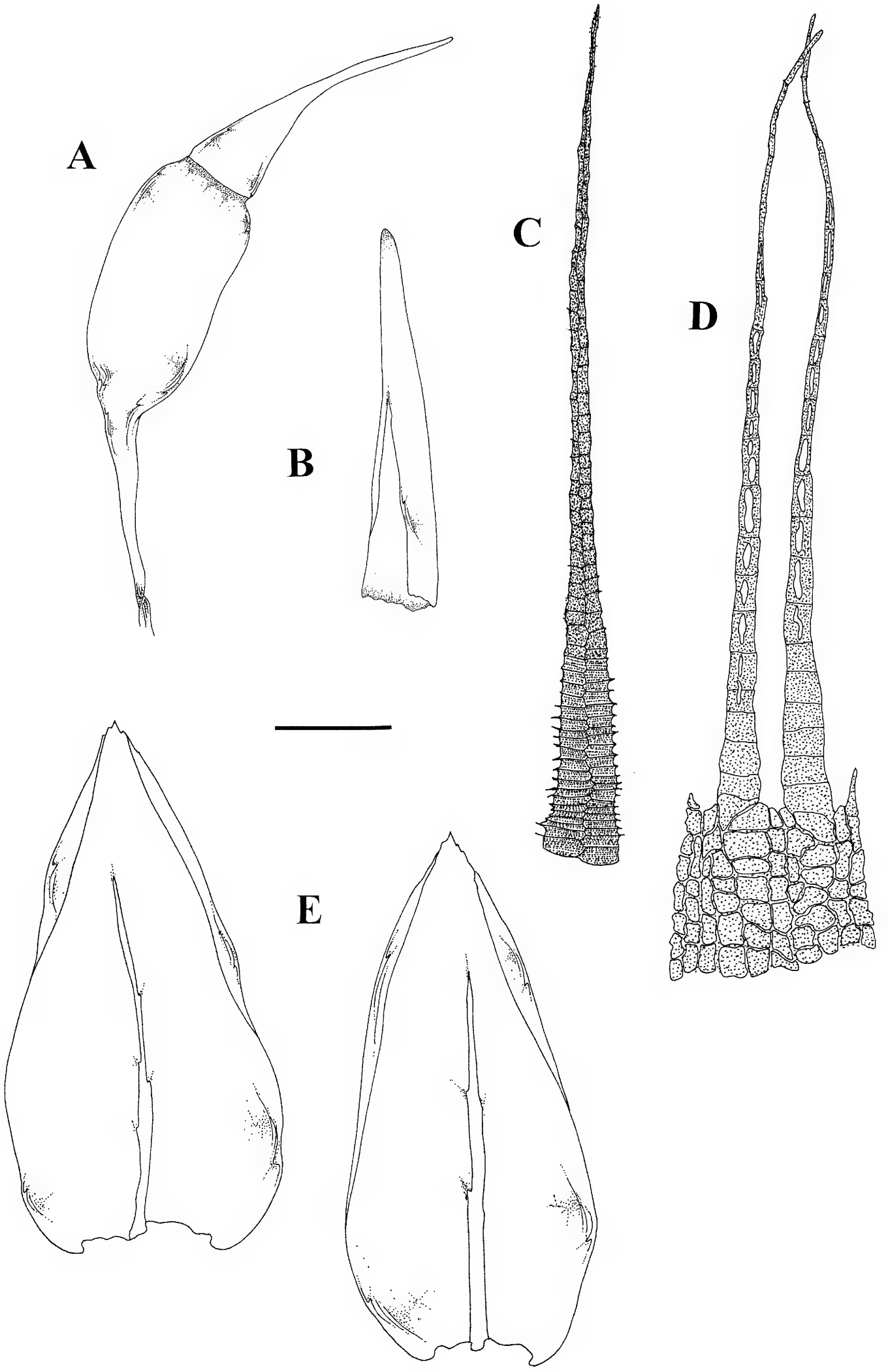


Figure 105. *Porotrichodendron superbum*. A. Seta, capsule, and operculum. B. Calyptra. C. Exostome, dorsal (outer) surface. D. Endostome, ventral (inner) surface. E. Stem leaves. Scale in mm: bar = 0.2 (C, D); bar = 0.5 (E); bar = 1.25 (A); bar = 1.3 (B). E from *Allen 12062*; all other figure parts from *Gómez 21822*.

Porotrichum porteri Cardot & Thér. *in* Thér., Revista Chilena Hist. Nat. 21: 18. 1917. *Porotrichodendron porteri* (Cardot & Thér.) Broth., Nat. Pflanzenfam. (ed. 2) 11: 206. 1925. Protologue. [Chile] San Javier, leg *C. E. Porter*, Févr. 1913, *N.º 11*. Type. Chile, San Javier, *Porter 11* (PC, holotype).

Eriodon longipes R. S. Williams, Field Mus. Nat. Hist., Bot. Ser. 4(5): 136. 1927. *Porotrichodendron longipes* (R. S. Williams) W. R. Buck, Brittonia 33: 559. 1981. Protologue. Tambo de Vaca, Peru, on trees, about 13,000 ft., June, 1923. *G. S. Bryan, no. 574*. Type. Peru, Tambo de Vaca, *Bryan 574* (NY, holotype).

Plants medium-sized to large, 3–20 cm long, yellowish to green or light green, glossy to dull. Stolons creeping; stems creeping to ascending and erect, stipitate, irregularly pinnate to bipinnate, complanate to terete-foliate, narrowed at tips, sometimes cuspidate; flagellate branchlets sometimes present. Pseudoparaphyllia foliose, broadly ovate, variable, ovate to lanceolate, rarely linear, serrate to serrulate on margins. Stipe leaves appressed to spreading, scarious. Stem leaves erect-spreading, complanate to somewhat concave, occasionally undulate, 1.5–3.0 × 0.6–1.5 mm, broadly acute to somewhat obtuse, often abruptly apiculate, rounded to slightly auriculate at base; margins irregularly serrate with unicellular or multicellular teeth near apex, serrate to serrulate in upper half, sometimes nearly entire, plane to incurved above; costae single, extending 2/3–3/4 the leaf length, sometimes ending in a small spine on the dorsal surface; cells smooth, rhombic near apex, 10–22 × 4–6 µm, linear-fusiform below, 20–50 × 3–5 µm, thin- to thick-walled below, thick-walled above, porose throughout; alar cells weakly differentiated, of 2–5 short-rectangular cells at the basal angles, cells across the insertions strongly porose, orange. Branch leaves erect-spreading, smooth, concave, oblong-lanceolate to oblong-ovate, 0.8–1.5 × 0.3–0.8 mm, abruptly acute, often apiculate, sometimes reddish or orange across insertions; margins irregularly serrate to serrulate above, sometimes incurved above, serrulate to entire below; costae single, extending 1/2–3/4 the leaf length, sometimes weak and nearly lacking; cells smooth, rhombic above, 12–28 × 2–6 µm, linear-fusiform below, 18–42 × 2–4 µm; alar cells weakly differentiated, of 2–5 short-rectangular cells at the basal angles, cells across the insertions strongly porose, orange to slightly reddish. Dioicous. Setae red, smooth, flexuose, 3.0–3.5 cm long. Capsules long-exserted, erect to inclined, ovoid, 1.5–3.0 mm long; exothecial cells short-rectangular to subquadrate, at times oblate, firm- to thick-walled; stomata superficial to somewhat immersed on capsule neck; opercula long-rostrate, 2–3 mm long; annuli large, compound, persistent on capsule mouth; peristome diplolepideous, inserted within the capsule mouth; exostome teeth pale whitish, becoming red with age, linear, to 1.4 mm long, dorsal (outer) lamellae striate-papillose below, densely papillose above, dorsal (outer) trabeculae below laterally extended and fringing the teeth, ventral (inner) lamellae lightly papillose below, densely papillose above; endostome yellow, basal membranes to 300 µm high, segments linear to 1.5 mm long, perforate, not keeled, lightly papillose, cilia 1–2, rudimentary or none. Spores irregularly round to somewhat oval, 12–16 µm, lightly papillose. Calyptrae cucullate, smooth or sparsely hairy when young, to 3 mm long.

Illustrations. Brotherus (1909, Fig. 895, as *Porotrichodendron mahahaicum*); Williams (1927, Pl. 10, as *Eriodon longipes*); Herzog (1916, Figs. 49–51); Brotherus (1925, Fig. 580, as *Porotrichodendron mahahaicum*); Bartram (1949, Fig. 129 A–D); Sharp *et al.* (1994, Fig. 571); Churchill and Linares (1995, Fig. 188 f–k); Buck (1998, Pl. 43 8–15); Gradstein *et al.* (2001, Fig. 216 I–Q). Figures 104, 105.

Habitat. On tree trunks, branches, vines, rotting logs, humus on forest floors, rarely on soil banks and rocks by waterfalls, often in misty or damp woods; 600–3200 m.

Distribution in Central America. GUATEMALA. Chimaltenango: *Standley 60035a* (F, FH); Huehuetenango: *Sharp 4960* (F, FH); Quetzaltenango: *Standley 85073a* (F); Sacatepéquez: *Kellerman s.n.* (FH, US); San Marcos: *Standley 86283* (F, FH). EL SALVADOR. Chalatenango: *Sipman 37645* (NY). HONDURAS. Comayagua: *Allen 12176* (MO); Cortés: *Allen 14263* (MO); Lempira: *Allen 12691* (MO, NY); Olancho: *Allen 12671* (MO). COSTA RICA. Cartago: *Davidse 24707* (MO); Heredia: *Crosby 10930* (MO, NY); Limón: *Davidse et al. 25908* (MO, NY); Puntarenas: *Gómez et al. 21828* (MO); San José: *Crosby & Crosby 5713* (F, MO). PANAMA. Chiriquí: *Croat 13780B* (F, FH, MO, NY, PMA, US).

World range: Mexico; Central America; Caribbean; Western, Northern, and Southern South America, Brazil; [?Malesia].

Porotrichodendron superbum is a large to medium-sized moss with usually weakly stipitate stems and noticeably red stems and branches. The species is extremely variable, and in Central America there are three distinct forms. The most common form has more or less slender, terete-foliate stems and branches. A second form of the species in Central America also has terete-foliate stem and branches, but the stem and branch leaves are lax and swollen in a manner similar to the turgid form of *Calyptothecium duplicatum*. *Calyptothecium duplicatum* differs from *P. superbum* in having ecostate leaves and filamentous pseudoparaphyllia. The third Central American form of *P. superbum* differs from the others in having complanate stem leaves. Other distinctive features of *P. superbum* include its often apiculate secondary stem and branch leaves that are clearly rounded to the insertions, with weakly developed alar cells, and long-linear leaf cells.

Porotrichodendron lindigii is typically a smaller plant than *P. superbum* (1.5–5 cm vs. 2–9 cm high), and it has strongly concave secondary stem and branch leaves. Although the branch leaves of *P. lindigii* and *P. superbum* are sometimes similar in shape, those of *P. lindigii* are usually cuspidate rather than apiculate. In addition, the apical leaf cells of *P. lindigii* are shorter (8–14 µm vs. 12–28 µm long) than those *P. superbum*, and rhombic in shape.

Porotrichodendron bertrandii is also a somewhat smaller species than *P. superbum* (2–5 cm vs. 2–9 cm high), but it has strongly stipitate secondary stems. Furthermore, the stem leaves of *P. bertrandii* are plicate, and the gradually acute branch leaves are lanceolate to oblong-lanceolate. Finally, the apical leaf cells of *P. bertrandii* are somewhat shorter (14–20 µm vs. 12–28 µm long) than those of *P. superbum*.

In the field *Porotrichodendron superbum* can be confused with *Pleurozium schreberi* or *Leptohymenium tenue* because all three species are similar in size and have a comparable aspect, distinctly red stems, and similar leaf shapes. The other two species, however, differ from *P. superbum* in having short, double costae. The leaves of *L. tenue* are also strongly plicate at base. *Porotrichum* species can generally be distinguished from *P. superbum* by their complanate-flattened secondary stem and branch leaves; however, as noted above, *P. superbum* sometimes has complanate stem leaves. Central American species of *Porotrichum* consistently differ from *P. superbum* in having leaves that are more or less straight rather than rounded to the insertions and branch leaves with one basal margin broadly incurved.

9. *Porotrichum* (Brid.) Hampe, Linnaea 32: 154. 1863. *Climacium* subgen. *Porotrichum* Brid., Bryol. Univ. 2: 275. 1827. *Thamnium* Schimp. *in* B.S.G. subgen. *Porotrichum* (Brid.) Kindb., Hedwigia 41: 210. 1902.

Hypnum Hedw. sect. *Dendroglossophyllum* Müll. Hal., Syn. Musc. Frond. 2: 223. 1851.
Thamnium subgen. *Camptolepis* Kindb. sect. *Trachyphylla* Kindb., Hedwigia 41: 212. 1902.
Porothamnium M. Fleisch., Musci Buitenzorg 3: 925. 1908.

Plants small, medium-sized, or robust, stipitate-frondose. Stolons creeping; rhizoids from circular clusters just below the leaf insertions, on stolons, and at the base of stipes; leaves widely spaced, evenly foliate. Stems erect, stipitate, irregularly pinnate, complanate-foliate, often flagellate-attenuate; stems in cross section with sclerodermis, enlarged cortical cells, central strand present; paraphyllia absent; pseudoparaphyllia foliose. Stipe leaves erect, erect-spreading, or squarrose, evenly foliate, margins plane or recurved. Stem leaves smooth or plicate to striate when dry, erect-spreading, strongly flattened, more or less symmetric, acute, obtuse, apiculate, mucronate, cuspidate or acuminate, shortly decurrent; margins weakly crenulate-denticulate, serrate or dentate at apex, more or less broadly inflexed below on one side, plane or narrowly recurved on the other; costae single or double, weak or strong, tapering at the ends or projecting as spines, at times spurred below, reaching 1/3–2/3 the leaf length, or percurrent; cells smooth or prorate, upper cells isodiametric, rounded-hexagonal, subquadrate, oblate-rhombic, or rhomboidal-fusiform, median cells rhomboidal-fusiform to fusiform-elongate; basal cells elongate-linear, cells at the extreme base porose; alar cells weakly differentiated, cells across the insertions yellow; branch leaves similar to stem leaves except smaller. Asexual reproduction by deciduous, flagellate branch tips or flagellate branches in leaf axils, or by deciduous leaves. Dioicous or gonioautoicous. Setae short or long, smooth to lightly roughened. Capsules exserted, erect to inclined, broadly-cylindrical to cylindrical; stomata present; opercula rostrate; peristome diplolepideous; exostome teeth on dorsal (outer) surface cross-striate below, papillose above;

endostome basal membranes high, segments keeled or plane, perforate, at times united at tips, cilia 1–3, nodose, rudimentary or absent. Calyptrae cucullate, smooth, naked.

Porotrichum is a genus of 36 species found primarily in the tropics, where it grows on tree trunks and branches, boulders, and rock outcrops. It has a stipitate habit with erect stems arising along well-developed stolons and usually complanate leaves with mostly unpitted (but sometimes porose) cells. Most species of *Porotrichum* reproduce asexually by means of deciduous, microphyllous, flagellate branches. The genus has exserted capsules, setae that are extremely variable in length, and its often reduced, diplolepideous peristomes have at least partially cross-striate exostomes. *Porotrichum* is mostly dioicous, and sporophytes are not often encountered. *Porotrichum* species may have as many as five different leaf morphologies: stolon, stipe, stem, branch, and flagellate branch leaves. Taxonomic characters of specific importance are found in the relative size of plants and leaves, stipe leaf stance, leaf shape, orientation of stipe, stem, and branch leaf margins, relative strength and length of the costae, leaf cell shape, and leaf margin dentation. Due in part to the variability of its leaf morphologies, the taxonomy of the group is unsettled. Furthermore, because many features of the *Porotrichum* gametophyte exhibit such broad variation, the genus, as presently understood, compromises the integrity of genera such as *Thamnobryum* and *Porotrichodendron*.

Porothamnium has been distinguished from *Porotrichum* on the basis of its more strongly cross-striate exostome, higher basal membrane, and better-developed endostomial cilia (Brotherus 1925). De Sloover (1983) further considered *Porothamnium* to have larger, darker green plants than *Porotrichum* and to have bright, fiery red setae rather than yellow, beige, orange, or dull red setae. Sastre (1987), Enroth (1994b), and Buck (1998) found no consistent or significant differences between the sporophytes or gametophytes of these genera that justified maintaining two genera. Central American species of this complex are quite variable in the features noted above.

The name *Porotrichum* combines the Greek *poros* (pore or opening) with *trich* (hair). According to Dixon (1904), the name refers to the perforations on the endostomial segments.

1. Stems and branches with distal leaves having percurrent costae that often expand to fill the apices . . . . . 2. *P. evansii*
1. All leaves with costae slender and tapering at tips, ending far below the apex 2

2. Stem leaves to 1 mm long; branch leaves to 0.6 mm long . . . . . 1. *P. brevifolium*
2. Stem leaves greater than 1.5 mm long; branch leaves greater than 0.6 mm long 3

3. Costae short and double or single and 1/3 the leaf length; plants gonioautoicous . . . . . 10. *P. tenuinerve*
3. Costae single, 1/2–3/4 the leaf length; plants dioicous 4

4. Cells in the upper 1/4 of the leaf hexagonal, subquadrate, or rhombic . . . . . 11. *P. usagarum*
4. Cells in the upper 1/4 of the leaf fusiform 5

5. Stipe leaf margins broadly recurved 6
5. Stipe leaf margins plane or weakly, irregularly, and obscurely recurved 7

6. Stipe leaves squarrose-recurved; stem leaves ovate-lanceolate; leaf costae strong throughout and often ending in a stout spine; leaf cells usually prorate . . . . . 9. *P. substriatum*
6. Stipe leaves spreading to wide-spreading; stem leaves oval-oblong; leaf costae tapering above, not ending in a spine; leaf cells smooth . . . . . 3. *P. filiferum*

7. Branch leaf margins narrowly recurved at base 8
7. Branch leaf margins plane at base 9

8. Leaves flexuose-crispate when dry; stem leaves to 2.5 mm long . . . . . 6. *P. longirostre*
8. Leaves complanate-flattened when dry; at least some stem leaves more than 3.0 mm long . . . . . 5. *P. lancifrons*

9. Plants often dark green, not or weakly branched; ultimate branch leaves obovate to spathulate, obtuse with rhombic, smooth apical cells . . . . . 4. *P. korthalsianum*
9. Plants pale green to yellow green, irregularly 1- or 2-pinnately branched; ultimate branch leaves ligulate, acute with long-flexuose, porose apical cells. 10

10. Setae 3–10 mm long. . . . . 7. *P. mutabile*
10. Setae 15–25 mm long . . . . . 8. *P. pittieri*

1. *Porotrichum brevifolium* E. B. Bartram, Bryologist 49: 117. 1946. Protologue. Guatemala. Dept. Alta Verapaz: vicinity of caves southwest of Lanquín, elev. 600–1000 m, *Steyermark 44098.* Types. Guatemala. Dept. Alta Verapaz, vicinity of caves southwest of Lanquín, elev. 600–1000 m, *Steyermark 44098* (FH, holotype; F, MO, US, isotypes).

Plants small and slender to medium-sized, to 4 cm high, stipitate-frondose, forming dark green to yellowish green, lax tufts. Stolons creeping; rhizoids smooth to lightly roughened, reddish brown, not or sparsely branched, in circular clusters just below the leaf insertions, on stolons, and at the base of stipitate stems; leaves loosely imbricate, widely spaced, evenly foliate, triangular. Stems erect, stipitate, irregularly pinnate, complanate-foliate, often flagellate-attenuate; stems in cross section with sclerodermis of 3–5 rows of small, thick-walled cells, grading into larger, firm-walled cortical cells, central strand very poorly developed; paraphyllia absent; pseudoparaphyllia foliose. Stipes evenly foliate; leaves appressed below, erect-spreading above, ovate-triangular to triangular, 0.6 mm long, acute to acuminate; margins entire to subserrulate; costae single and strong, ending 1/2–2/3 the leaf length. Stem leaves 0.7–1.3 mm long, erect-spreading, flattened, oblong-lingulate, more or less symmetric, broadly rounded to obtuse, apiculate or mucronate, shortly decurrent; margins weakly crenulate-denticulate above, more or less broadly inflexed below on one side, plane or narrowly recurved on the other; costae single, weak, tapering at the ends, 1/2–2/3 the leaf length; cells smooth, upper cells isodiametric, rounded-hexagonal, rhombic, subquadrate, or oblate, 6–14 µm long, median cells rhomboidal-fusiform to fusiform-elongate, 16–40 × 4–6 µm; basal cells elongate-linear, cells at the extreme base porose; alar cells weakly differentiated as a few oblate, quadrate, or short-rectangular cells at the basal angles, cells across the insertions yellow; branch leaves similar to stem leaves except smaller. Asexual reproduction by axillary, microphyllous, flagelliform branches. Dioicous (?). Sporophytes unknown.

Illustrations. Bartram (1949, Fig. 128 D–F). Figure 106.

Habitat. On rocks and boulders in stream beds and around spring outlets, seeping cliff faces, and on bark at base of trees; 120–1000 m.

Distribution in Central America. BELIZE. Toledo: *Whittemore 57229* (MO). GUATEMALA. Alta Verapaz: *Steyermark 44098* (F, FH, MO, US). HONDURAS. Atlántida: *Allen 17278* (MO). COSTA RICA. Heredia: *Crosby 9925* (MO). PANAMA. Coclé: *Witherspoon & Witherspoon 8767* (MO).

World range: Central America.

Porotrichum brevifolium is the smallest species of *Porotrichum* in Central America. It has oblong-lingulate, broadly rounded to obtuse leaves that are apiculate or minutely mucronate. The leaf margins are weakly crenulate-denticulate above, consistently inflexed on one side below, and may or may not be narrowly recurved on the other. The upper leaf cells in *P. brevifolium* are short, but extremely variable in shape: isodiametric, rounded-hexagonal, rhombic, subquadrate, or oblate. The median leaf cells are rhomboidal-fusiform to fusiform-elongate. The collections of this species often have flagellate-attenuate secondary stems and branches as well as numerous axillary, microphyllous, flagelliform branches.

The combination of its small leaf size and short, often isodiametric, upper leaf cells immediately distinguishes *P. brevifolium* from the other Central American species of *Porotrichum*. Although *P. usagarum* also has short upper leaf cells, it is a more robust plant with coarsely serrate stem leaves that can reach 2.0 mm in length. *Porotrichum brevifolium* is more likely to be confused with *Homaliodendron piniforme* or *Pinnatella minuta*, since they all are more or less similar in size. These species

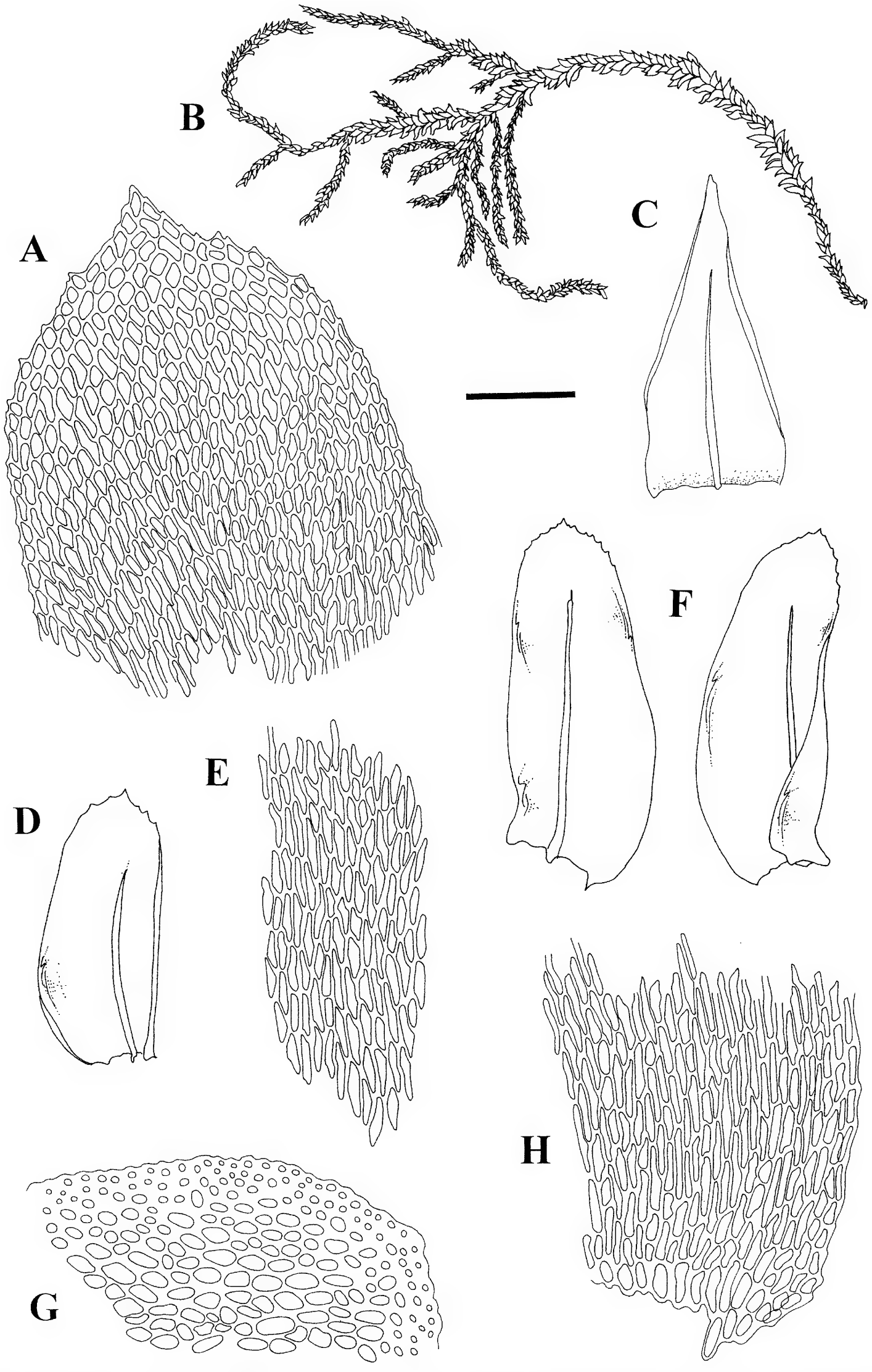


Figure 106. *Porotrichum brevifolium*. A. Leaf apex. B. Habit. C. Stipe leaf. D & F. Stem leaves. E. Median leaf cells. G. Stem in cross section. H. Basal and alar cells. Scale in mm: bar = 0.06 (A, E, G, H); bar = 0.2 (C); bar = 0.4 (D, F); bar = 4.3 (B). All figure parts from *Steyermark 4409* (type).

differ from *Porotrichum brevifolium* in having short, often isodiametric, median leaf cells. *Pinnatella minuta* also differs from *P. brevifolium* in having stronger costae, serrulate upper leaf margins, and an intramarginal limbidium in the basal region of its leaves. Furthermore, *Homaliodendron piniforme* differs from *P. brevifolium* in having oblong-ovate, asymmetric stem leaves, and in lacking a stem central strand.

2. *Porotrichum evansii* B. H. Allen, *sp. nov.* Type. Honduras. Yoro: Cordillera Nombre de Dios. North slope, ridge between Rio Guán Guán and Quebrada Aguacatal. 15°30′N, 87°28′W, 100–300 m, *Allen 13491* (MO, holotype; NY, TEFH, isotypes).

Species haec a congeneris foliis superis cum costis percurrentibus differt.

Plants medium-sized, to 4 cm high, stipitate-frondose, forming dull green to dark green, lax tufts. Stolons creeping; rhizoids smooth to lightly roughened, reddish brown, not or sparsely branched, in circular clusters just below the leaf insertions, on stolons, and at the base of stipitate stems; leaves loosely imbricate, widely spaced, evenly foliate, triangular. Stems erect, stipitate, irregularly pinnately branched, complanate-foliate, at times flagellate-attenuate; stems in cross section with sclerodermis of 5–8 rows of small, thick-walled cells, grading into larger, firm- to thick-walled cortical cells, central strand present; paraphyllia absent; pseudoparaphyllia foliose. Stipes evenly foliate; leaves widely spaced, erect-spreading to spreading, triangular to triangular-lanceolate, 0.6–0.7 mm long, acute; margins entire to subserrulate, plane; costae single and strong, ending 1/2–2/3 the leaf length. Stem leaves 1.2–1.5 mm long, erect-spreading, flattened, oblong-ovate to oblong-spathulate, more or less symmetric, broadly acute, mucronate to cuspidate, shortly decurrent; margins serrate above, entire below, more or less broadly inflexed below on one side, plane on the other; costae smooth on the dorsal surface, extremely variable in form: on lower leaves tapering at the ends, 2/3 the leaf length, higher up sometimes discontinuous (present only below and at the apex), on upper leaves percurrent, filling the mucro; cells smooth, upper cells rhombic to rhomboidal-fusiform, 16–26 × 4–6 µm, median cells rhomboidal, rhomboidal-fusiform to fusiform-elongate, 22–42 × 4–6 µm; basal cells elongate-linear, thick-walled; alar cells not or very weakly differentiated as a few quadrate or short-rectangular cells at the basal angles, cells across the insertions yellowish; branch leaves similar to stem leaves except smaller and more often oblong-spathulate. Dioicous(?). Sporophytes unknown.

Illustration. Figure 107.

Habitat. On boulders in woods and near streams, sides of vertical cliff faces, and occasionally on tree trunks and branches; 100–550 m.

Distribution in Central America. GUATEMALA. Izabal: *Steyermark 39151* (F). HONDURAS. Atlántida: *Allen 17236* (MO); Yoro: *Allen 13491* (MO, NY, TEFH). COSTA RICA. Limón: *Holm 1272* (MO). PANAMA. Bocas del Toro: *Allen 5530* (MO); Canal Area: *Steyermark & Allen 17201* (MO); Chiriquí: *Allen 5496* (MO); Colón: *Crosby 10462* (MO); Panamá: *Crosby 4549B* (MO); Darién: *Allen 8736* (MO, NY).

World range: Central America.

Porotrichum evansii is a small to medium-sized species of pale to dark green plants with strongly complanate, well-spaced leaves. Its leaves are mostly oblong-ovate, sharply serrate above, and mucronate to cuspidate. It differs from all Central American species of *Porotrichum* by virtue of its remarkably variable leaf costae. The leaves in the lower parts of the stems and branches have costae that reach 1/2–2/3 the leaf length. Further up the stems and branches, the leaves sometimes have discontinuous costae, *i.e.*, present in the lower parts of the leaves and filling the apex, but absent in between. The leaves on the upper parts of the stem and branches have percurrent costae that often expand in the apex to fill the mucros or cusps.

Thamnobryum typically differs from *Porotrichum* in having a dark green color, strong, percurrent to subpercurrent costae, and short, often rhombic to subquadrate upper leaf cells. *Porotrichum evansii*, therefore, causes significant problems in distinguishing the two genera since collections of it can be pale or dark green, and have costae that either end at half the leaf length or are percurrent. It differs from *Thamnobryum* only in having somewhat longer upper leaf cells. As a generic feature, how-

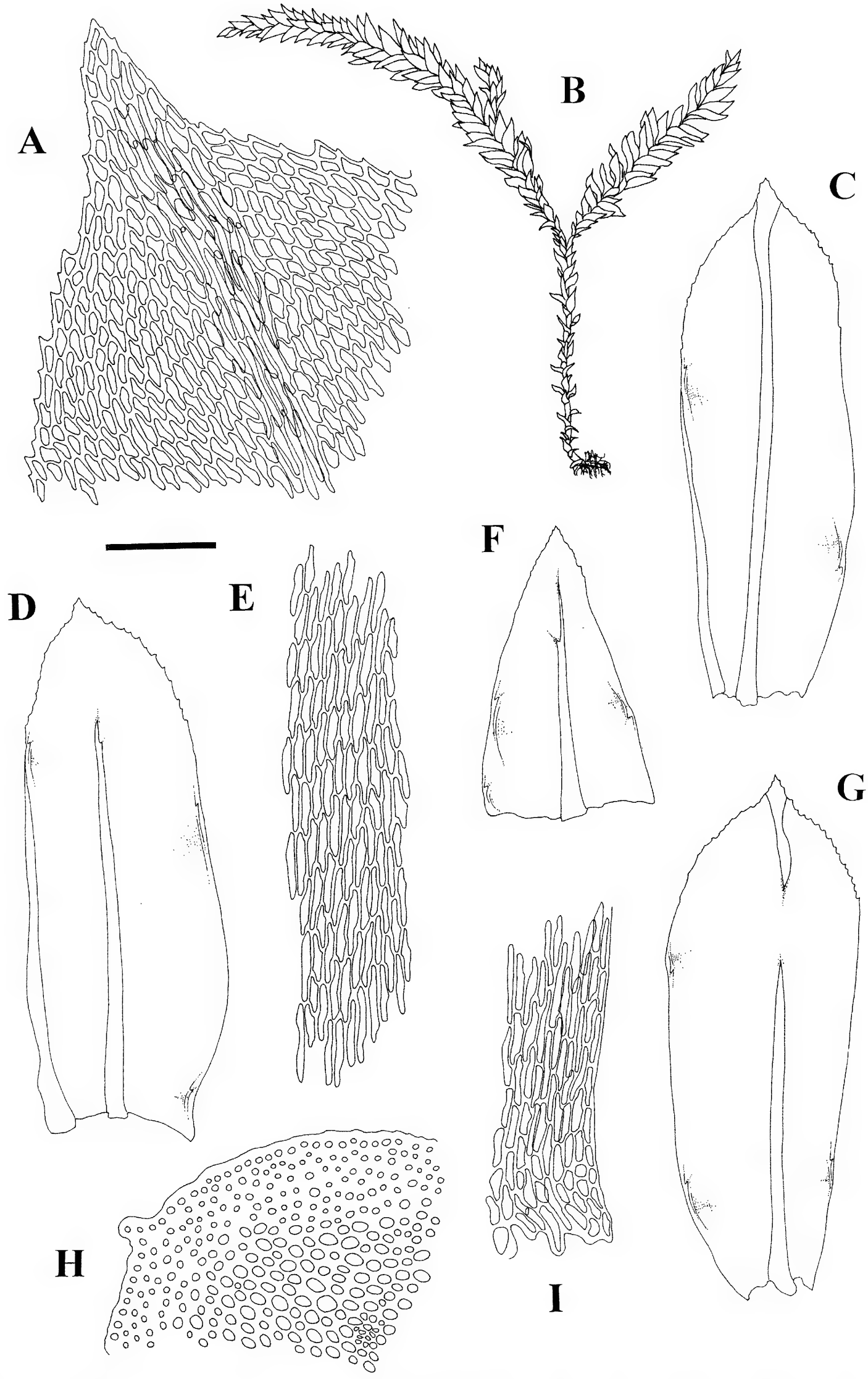
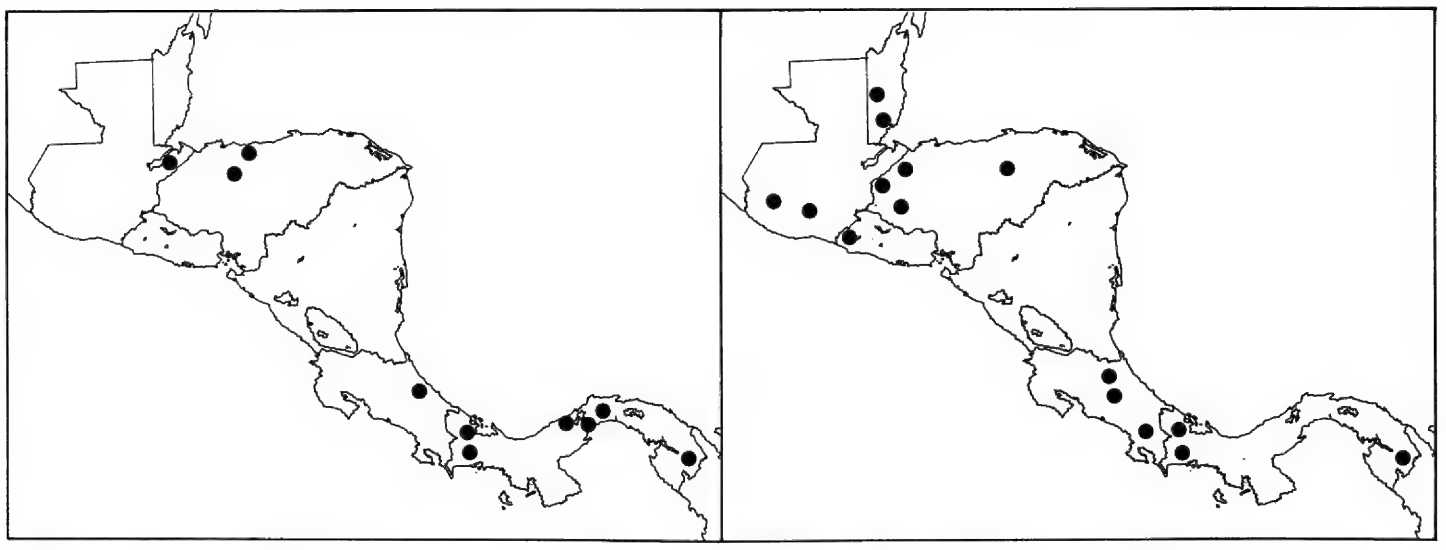


Figure 107. *Porotrichum evansii*. A. Leaf apex. B. Habit. C, D & G. Stem leaves. E. Median leaf cells. F. Stipe leaf. H. Stem in cross section. I. Basal and alar cells. Scale in mm: bar = 0.06 (A, E, H, I); bar = 0.26 (C, D, F, G); bar = 4.0 (B). All figure parts from *Allen 13491* (type).



Porotrichum evansii *Porotrichum filiferum*

ever, short leaf cells alone do not distinguish *Thamnobryum* from *Porotrichum* since *P. usagarum* has short leaf cells identical to those found in *Thamnobryum*.

3. *Porotrichum filiferum* Mitt., J. Linn. Soc., Bot. 12: 468. 1869. *Thamnium filiferum* (Mitt.) M. Fleisch. *in* Broth., Nat. Pflanzenfam. (ed. 2) 11: 199. 1925. Protologue. Hab. Venezuela, *Funck et Schlim*; Andes Quitenses, ad flumen Bombonasa (1500 ped.), *Spruce*, n. 1365. Andes Peruvianae, ad rivulum Shillicaio (2000 ped.), *Spruce*, 1366; ad Tarapota (1600 ped.), *Spruce*, n. 1367. Types. Ecuador. Bombonasa, *Spruce 1365* (NY, lectotype, designated here); Peru: Chillicaio [sic], *Spruce 1366* (NY, syntype); Tarapota, *Spruce 1367* (NY, syntype). Venezuela, *Funck & Schlim* (NY, syntype; not MO).

Plants small to medium-sized, 2.5–6 cm high, stipitate-frondose, forming pale green to dark green, lax tufts. Stolons creeping, evenly foliate; rhizoids smooth to lightly roughened, red to reddish brown, not or sparsely branched, in circular clusters just below the leaf insertions, on stolons, and at the base of stipitate stems; leaves imbricate, widely spaced, triangular, ecostate, 0.3–0.5 mm long. Stems erect, stipitate, irregularly pinnate, frondose to complanate-foliate, at times flagellate-attenuate; stems in cross section with sclerodermis of 4–5 rows of small, thick-walled cells, grading into larger, firm-walled cortical cells, central strand present; paraphyllia absent; pseudoparaphyllia subfoliose to nearly filiform. Stipes evenly foliate; leaves appressed below, spreading to recurved above, ovate-triangular to triangular, 0.6–1.0 mm long, acute to acuminate, margins entire to subserrulate, recurved below; costae single and weak, 1/2 the leaf length. Stem leaves 1.5–2.0 mm long, more or less plicate to striate when dry, erect-spreading, flattened, oblong to oblong-ovate, more or less symmetric, broadly acute to obtuse, apiculate, shortly decurrent; margins serrate to serrulate above, serrulate to subentire below, below on one side inflexed then narrowly recurved, plane or narrowly recurved on the other; costae single, tapering at the ends, not or rarely projecting at tips, 2/3–3/4 the leaf length; cells smooth or prorate, upper cells hexagonal to rhomboid-fusiform, 14–24 × 4–6 µm, median cells elongate-fusiform, 35–50 × 4–6 µm; basal cells elongate-linear, cells at the extreme base porose; alar cells weakly differentiated as a few oblate, quadrate, or short-rectangular cells at the basal angles, cells across the insertions yellow; branch leaves wide-spreading, flattened, similar to stem leaves except smaller. Asexual reproduction by axillary, microphyllous, flagelliform branches. Dioicous. Perigonia lateral on branches, 1 mm long. Perichaetia lateral on stems and branches, 1.0–1.5 mm long; leaves convolute at base, spreading above, abruptly long-acuminate; margins subentire; costae absent. Setae 15–20 mm long, red, smooth. Capsules erect to suberect, oblong-cylindrical to ovate-cylindrical, 1.7–2.0 mm long; exothecial cells oblong to short-rectangular, thick-walled; stomata present; opercula long conic-rostrate, 1.5 mm long; annuli complex, of 2–3 rows of enlarged, thin-walled cells clinging to capsule mouth or deciduous but not revoluble; peristome diplolepideous; exostome teeth pale yellow, dorsal surface cross-striate and papillose below, papillose above; endostome pale yellow to hyaline, as long as exostome teeth, papillose, basal membranes high, segments

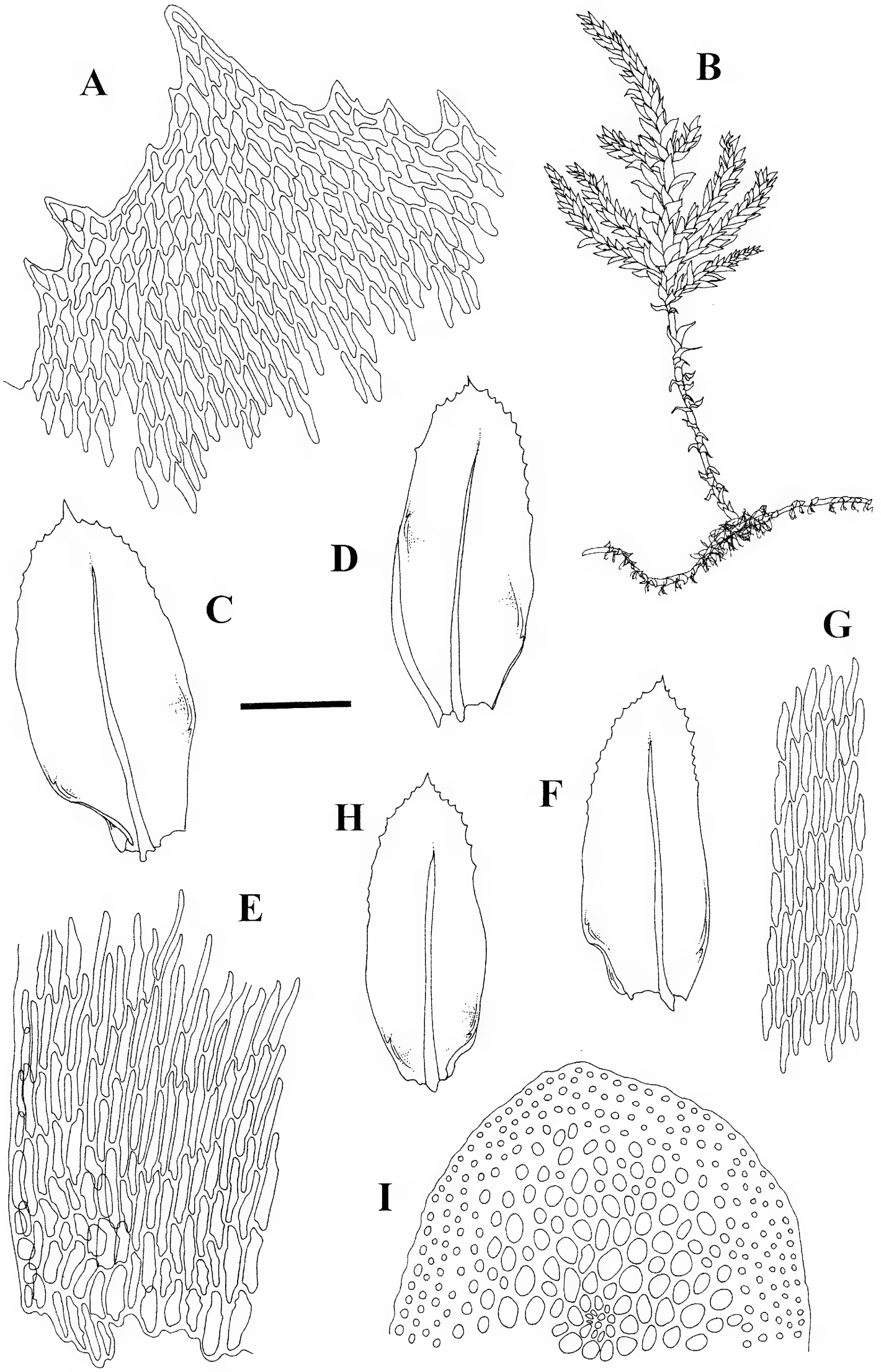


Figure 108. *Porotrichum filiferum*. A. Leaf apex. B. Habit. C & D. Stem leaves. E. Basal and alar cells. F & H. Branch leaves. G. Median leaf cells. I. Stem in cross section. Scale in mm: bar = 0.06 (A, E, G, I); bar = 0.5 (C, D, F, H); bar = 5.0 (B). All figure parts from *Allen 8910*.

broadly perforate, cilia rudimentary. Spores lightly papillose, 12–18 µm. Calyptrae 2.5–3.0 mm long, yellow, cucullate, smooth, naked.

Illustration. Figure 108.

Habitat. On tree trunks, branches, and roots; 20–2100 m.

Distribution in Central America. BELIZE. Cayo: *Allen 18022* (MO); Toledo: *Allen 18581* (MO). GUATEMALA. Quetzaltenango: *Steyermark 35161* (F, FH); Sacatepéquez: *Standley* 88960 (F, FH). EL SALVADOR. Ahuachapán: *Davidse et al. 37467* (MO). HONDURAS. Copán: *Allen 17746* (MO); Lempira: *Allen 11992B* (MO); Olancho: *Allen 12415* (MO); Santa Bárbara: *Crosby 2790* (MO). COSTA RICA. Cartago: *Standley & Valerio 46877a* (FH, US); Heredia: *Crosby 9927* (MO); Puntarenas: *Croat 26672* (CR, MO). PANAMA. Bocas del Toro: *Allen 5105A* (MO); Chiriquí: *Croat 15890C* (MO); Darién: *Allen 8910* (MO).

World range: Central America; Western and Northern South America, Brazil.

Porotrichum filiferum is a small to medium-sized species found on bark or rotting logs rather than rocks. It has well-developed stipes with spreading to somewhat reflexed leaves that have distinctly recurved margins. The stem and branch leaves in *P. filiferum* are mostly complanate, more or less plicate when dry, oblong to oblong-ovate, and at base broadly incurved on one side, then abruptly and shortly recurved. The upper leaf cells are short, hexagonal to rhomboid-fusiform, and smooth. The costae in *P. filiferum* are long and single, but taper at the ends and rarely end in a projecting point.

Porotrichum substriatum is the only other Central American species of *Porotrichum* with stipe leaves that have distinctly recurved margins. It differs from *P. filiferum* in having squarrose-recurved stipe leaves and evenly foliate, ovate-lanceolate leaves that have stoutly spined costae and prorate leaf cells.

Porotrichum lancifrons and *P. longirostre* are similar to *P. filiferum* in having secondary stem and branch leaves that at base are broadly incurved on one side, then abruptly and shortly recurved. These species are considerably larger than *P. filiferum* and they have broadly triangular, mostly appressed stipe leaves with plane margins.

Mitten (1869) listed four syntypes for *P. filiferum.* The species is here lectotypified with Andes Quitenses, ad flumen Bombonasa (1500 ped.), *Spruce*, n. 1365 (NY). A duplicate of one syntype in MO (Venezuela, *Funck et Schlim*, MO) contains only plants of *P. usagarum.*

4. *Porotrichum korthalsianum* (Dozy & Molk.) Mitt., J. Linn. Soc., Bot. 12: 463. 1869. *Neckera korthalsiana* Dozy & Molk., Pugillus Sp. Nov. Fl. Bryol. Venez. *in* Prodr. Fl. Bryol. Surinam. [Natuurk. Verh. Holl. Maatsch. Wetensch. Haarlem II, 10(3):] 42. 1854. Protologue. Habitat: in Venezuela ad terram, in sylvis juxta Rio Catuche, [*P. W. Korthals*].

Porotrichum cobanense Müll. Hal., Bull. Herb. Boissier 5: 202. 1877. *Thamnium cobanense* (Müll. Hal.) R. S. Williams, Contr. U.S. Natl. Herb. 16: 24. 1912. Protologue. [Guatemala] Habitatio. In sylva primaeva prope Coban ad arbores, 4800 ped. altum: *H. v. Türckheim* 14 Febr. 1886 sterile legit. Hb. Levier.

Plants medium-sized, 3–8 cm high, stipitate-frondose, forming dark green to green, lax tufts. Stolons creeping, evenly foliate; rhizoids smooth to lightly roughened, red to reddish brown, sparsely and irregularly branched, in dense circular clusters just below the leaf insertions, on stolons, and at the base of stipitate stems; leaves erect to erect-spreading, widely spaced, ovate-triangular to triangular, 0.3 mm long. Stems erect, stipitate, irregularly and weakly 1–2-pinnate, complanate-foliate; stems in cross section with sclerodermis of 5–6 rows of small, red, thick-walled cells, grading into larger, yellow to hyaline, firm- or thick-walled cortical cells, central strand present; paraphyllia absent; pseudoparaphyllia foliose. Stipes evenly foliate; leaves appressed below, erect-spreading above, becoming progressively larger from the base to the first branch, 1.0–1.5 mm long at mid-stipe, ovate-triangular to triangular, acute to acuminate; margins entire to subserrulate, plane; costae strong, 3/4 the leaf length. Stem leaves 2–3 mm long, flattened, spreading, often striate-plicate when dry, oblong-ovate or ovate-ligulate, somewhat asymmetric, obtuse-apiculate to broadly acute; margins serrate or dentate at apex, teeth mostly 1-celled, sometimes of 2–3 cells, serrulate to subentire below, broadly incurved below on one side; costae single (occasionally double), 2/3–3/4 the leaf length,

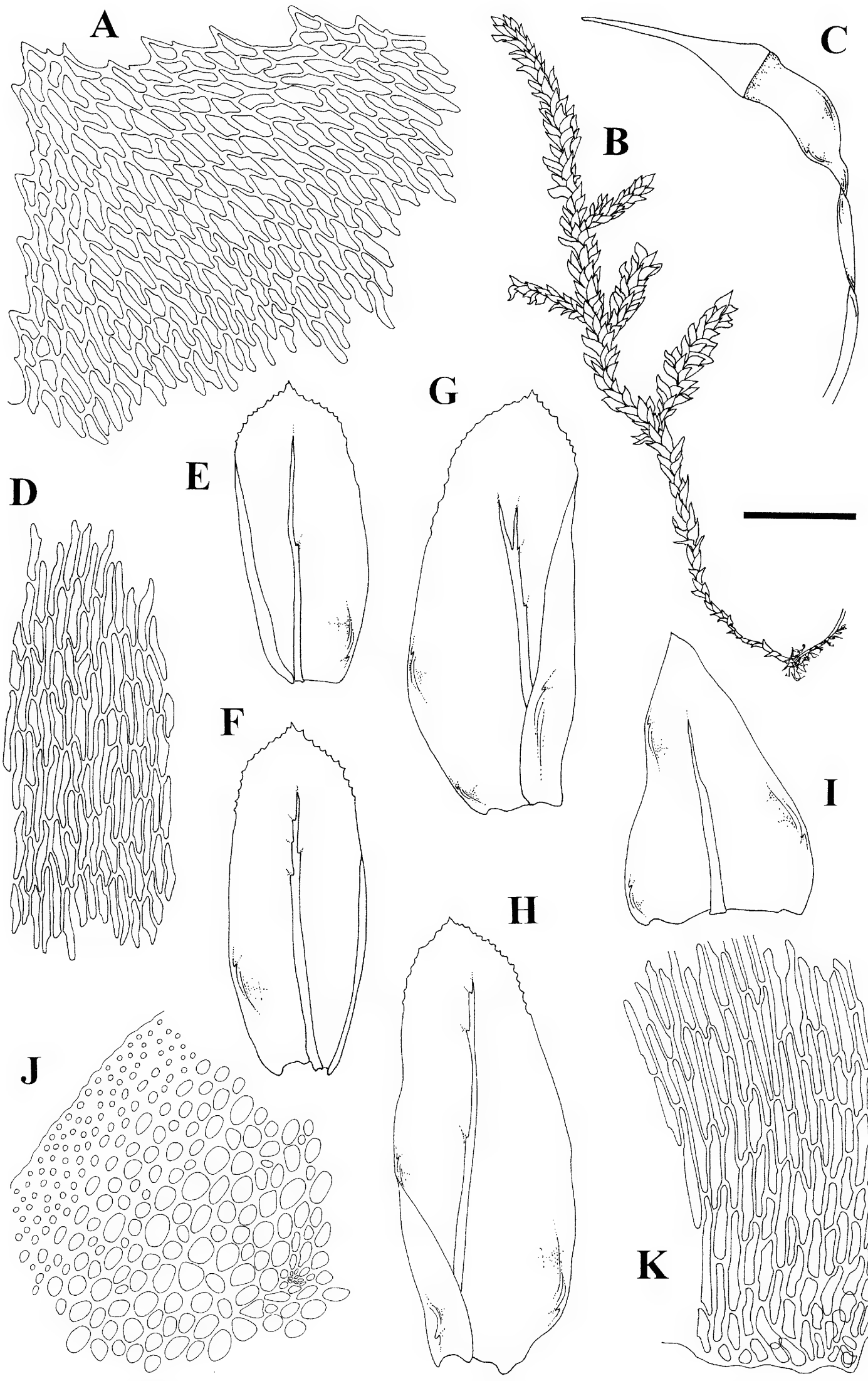
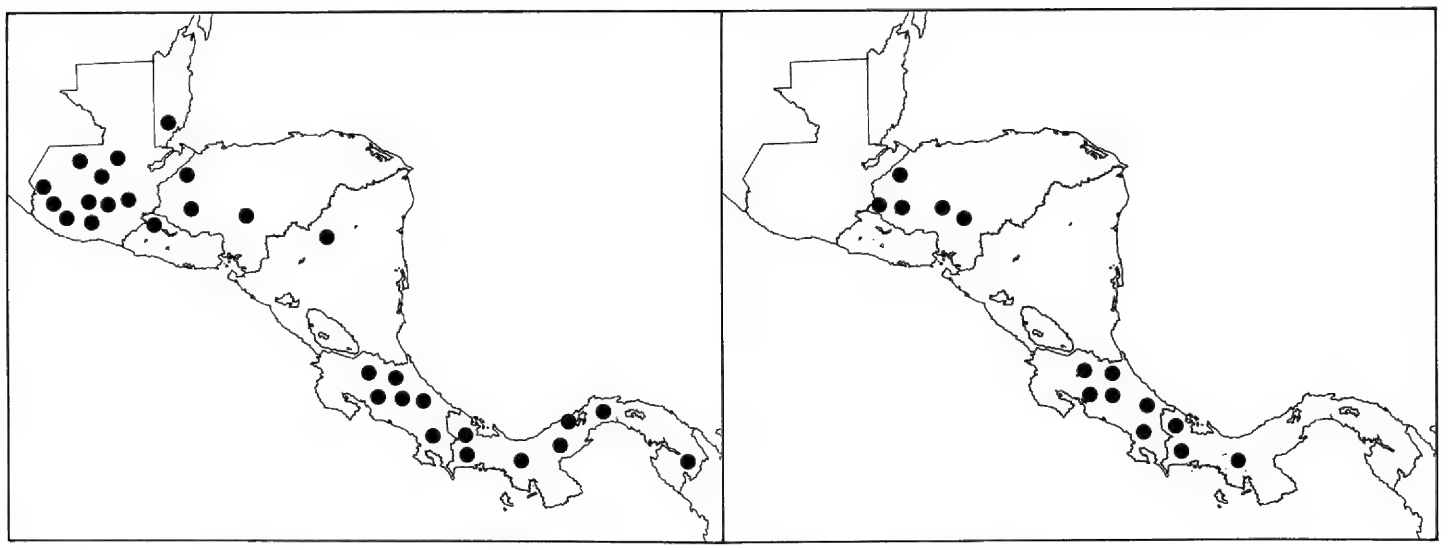


Figure 109. *Porotrichum korthalsianum*. A. Leaf apex. B. Habit. C. Seta, capsule, and operculum. D. Median leaf cells. E & F. Branch leaves. G & H. Stem leaves. I. Stipe leaf. J. Stem in cross section. K. Basal and alar cells. Scale in mm: bar = 0.06 (A, D, K); bar = 0.08 (J); bar = 0.5 (E–I); bar = 1.3 (C); bar = 8.0 (B). C from *Davidse 29119*; all other figure parts from *Allen 11398*.



Porotrichum korthalsianum *Porotrichum lancifrons*

broad at base, tapering above, often spurred below, not or rarely weakly ending in a spine; cells smooth, upper cells rhomboidal, 12–24 × 4–8 µm, median and basal cells elongate-fusiform to short-vermicular, 24–70 × 4–6 µm; alar cells subrectangular to subquadrate, thick-walled, porose, yellow red, cells across the insertions porose and yellow; branch leaves erect-spreading to spreading, flattened, oblong-ovate, oblong-ligulate, occasionally spathulate, acute, 1–2 mm long, otherwise similar to secondary stem leaves. Asexual reproduction occasionally by deciduous, flagellate branch tips or flagellate branches in leaf axils. Dioicous. Setae 10–25 mm long, yellow, becoming red to reddish brown with age, smooth. Capsules erect to inclined, broadly-cylindrical to cylindrical, constricted to wrinkled at neck, 1–2 mm long; exothecial cells small, thick-walled at mouth, rounded-rectangular to rectangular below, firm- to thick-walled; stomata on neck; opercula conic at base, obliquely long-rostrate above, 1–3 mm long; annuli complex, of 2–3 rows of enlarged, thin-walled cells, deciduous but not revoluble; peristome diplolepideous; exostome teeth narrowly triangular, reddish below, pale yellow above, dorsal surface papillose and cross-striate below, coarsely papillose above, trabeculae and median line thin below, thickened above, ventral surface with projecting trabeculae, lightly papillose; endostome pale yellow, lightly papillose below, densely papillose above, basal membranes high, segments linear, not or weakly keeled, broadly perforate, at times united at tips, cilia absent or rudimentary. Spores spherical, lightly papillose, 12–14 µm. Calyptrae 2.5–3.0 mm long, yellow, cucullate, smooth, naked.

Illustrations. Dozy and Molkenboer (1854, Pl. 9); Bartram (1949, Fig. 128 A–C); Florschütz-de Waard (1986, Fig. 111); Sharp *et al.* (1994, Fig. 568 d–g); Churchill and Linares (1995, Fig. 190 h–l); Duarte Bello (1997, Pl. 215); Buck (1998, Pl. 49); Buck (2003, Fig. 107). Figure 109.

Habitat. On boulders (limestone and granite) along streams and often wet limestone cliffs, occasionally on bark of tree trunks and buttress roots, logs, stumps, and soil banks; 660–3400 m.

Distribution in Central America. BELIZE. Toledo: *Allen 18758* (BRH, MO). GUATEMALA. Alta Verapaz: *Standley* 90071 (F, FH, MO); Baja Verapaz: *Sharp 2701* (FH, MO); Escuintla: *Standley 61315* (F, FH); Guatemala: *Svihla 2875* (FH); Jalapa: *Steyermark 32488* (F); Quetzaltenango: *Standley 85468* (F, FH, US); Quiché: *Sharp 2386* (MO); Sacatepéquez: *Standley 63695* (F); San Marcos: *Standley 86501* (F, FH); Suchitepéquez: *Holdridge s.n.* (MO). EL SALVADOR. Santa Ana: *Watson ES-0070* (MO). HONDURAS. Lempira: *Allen 11416* (MO); Francisco Morazán: *Standley 14097* (F); Santa Bárbara: *Allen 11654* (MO). NICARAGUA. Jinotega: *Standley 10742* (F, FH). COSTA RICA. Alajuela: *Lyon 612* (MO); Cartago: *Standley 51190* (US); Heredia: *Crosby 9891* (CR, MO, NY); Limón: *Davidse & Herrera 29119* (MO); Puntarenas: *Crosby 9950* (MO); San José: *Crosby & Crosby 6246* (MO). PANAMA. Bocas del Toro: *Allen 5088* (MO); Chiriquí: *Nee 10604* (MO, PMA); Coclé: *Crosby 4413* (MO); Colón: *Crosby 10389* (MO); Darién: *Allen 8987* (MO); Panamá: *Crosby 4496* (MO); Veraguas: *Crosby 10276* (MO).

World range: Mexico; Central America; Caribbean; Western and Northern South America, Brazil.

Porotrichum korthalsianum is a medium-sized species that typically is dark green in color and is usually found on rocks, boulders, or exposed rock faces. Its stems are usually weakly, irregularly 1-pinnately branched, and its erect to erect-spreading stipe leaves have plane margins. The stem and branch leaves are complanate, oblong-ovate or ovate-ligulate, obtuse-apiculate to broadly acute at the apex, and the margins are broadly incurved below on one side, but otherwise plane. Its costae are often spurred, and rarely end in spines. Typically, the apical stem and branch leaf cells are rhomboidal and smooth; however, the cells are sometimes weakly porose. Deciduous, flagellate branches are sometimes found in the species.

Porotrichum korthalsianum is superficially very similar to *Thamnobryum* in color, branching pattern, and overall plant aspect. It differs from that genus in having thinner costae that end well below the apex and longer upper leaf cells. *Porotrichum mutabile* usually differs from *P. korthalsianum* in its light green to yellowish color, more strongly and consistently branched stems, often equally foliate branch leaves, and common presence of deciduous flagelliform branches. The two species, however, are similar in size, with identical stipe leaves, more or less similar stem leaves, and branch leaves that are broadly incurved below on one side, but otherwise plane. *Porotrichum mutabile* further differs from *P. korthalsianum* in having narrower, often acute branch leaves with consistently longer, porose apical cells. *Porotrichum mutabile*, however, has incredibly variable branch leaves, and some difficulty in separating the two species is to be expected since the leaves of *P. mutabile* and *P. korthalsianum* are sometimes identical.

Porotrichum longirostre is similar to *P. korthalsianum* in size and in having erect-spreading to spreading, plane-margined stipe leaves. It differs in having leaves that are crispate when dry, and it often has longer stipes. The best features for distinguishing the two species, however, are found in the branch leaves. In *P. longirostre* the branch leaves are fairly consistently elliptic and are broadly inflexed below on one side, but then the margins are narrowly recurved on one or both sides. This feature is apparent under microscopic examination of both attached and detached leaves, and causes the leaves to be "strikingly narrower at the insertion" (Buck 1998).

5. *Porotrichum lancifrons* (Hampe) Mitt., J. Linn. Soc., Bot. 12: 462. 1869. *Hypnum lancifrons* Hampe, Linnaea 32: 158. 1863. *Thamnium lancifrons* (Hampe) Kindb., Hedwigia 41: 235. 1902. *Porothamnium lancifrons* (Hampe) M. Fleisch. *ex* Broth., Nat. Pflanzenfam. (ed. 2) 11: 199. 1925. Protologue. [Colombia] Hab. In sylv. Manzanos, 2700 metr., Julio, [*A. Lindig*] *no. 2117*.

Hypnum neckeraeforme Hampe, Ann. Sci. Nat. Bot., sér. 5, 5: 309. 1866. *Porotrichum neckeraeforme* (Hampe) Mitt., J. Linn. Soc., Bot. 12: 464. 1869. *Thamnium neckeraeforme* (Hampe) Kindb., Hedwigia 41: 226. 1902. *Porothamnium neckeraeforme* (Hampe) M. Fleisch. *ex* Broth., Nat. Pflanzenfam. (ed. 2) 11: 199. 1925. Protologue. [Colombia] Hab. Bogota, Choachi, 2600 m., in sylvis, sept. 1860, semel leg. *A. Lindig*.

Porotrichum crassipes Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32(1): 185. 1894. *Porothamnium crassipes* (Renauld & Cardot) M. Fleisch. *ex* Broth., Nat. Pflanzenfam. (ed. 2) 11: 199. 1925. Protologue. [Costa Rica] Forêts de l'Irazu; un seul spécimen, en mélange parmi d'autres Mousses (*Pitt.*[*ier*] *n° 5652*). Type. Plantae costaricenses exsiccatae *N° 5652*. Forêts de l'Irazu, 10/2 1891, legit (*H. Pittier*) ad *Tonduz* [Herb. J. Cardot] (PC, isotype), *syn. nov.*

Plants robust, to 13 cm high, stipitate-frondose, stipe sometimes longer than the frond, forming green to pale green, lax tufts. Stolons creeping; rhizoids smooth to lightly roughened, red to reddish brown, sparsely and irregularly branched, in dense circular clusters just below the leaf insertions, on stolons, and at the base of stipitate stems; leaves appressed, widely spaced, evenly foliate, ovate-triangular to triangular, 0.5–1.0 mm long. Stems erect, stipitate, irregularly 2–3-pinnate, complanate-foliate; stems in cross section with sclerodermis of 5–8 rows of small, thick-walled cells, grading into larger, firm- or thick-walled cortical cells, central strand well developed; paraphyllia absent; pseudoparaphyllia foliose. Stipes evenly foliate; leaves appressed below, erect-spreading above, becoming progressively larger from the base to the first branch, 1.0–1.5 mm long at mid-stipe, ovate-triangular to triangular, obtuse-cuspidate, entire to subserrulate; margins plane; costae 3/4 the leaf length. Stem leaves 2.0–3.5 mm long, flattened, spreading, often striate-plicate when dry, oblong-ovate, somewhat asymmetric, broadly acute, broadly apiculate; margins serrate or dentate at apex, teeth mostly 1-celled, sometimes of 2–3 cells, serrulate to well below midleaf; costae single, 2/3 the leaf length,

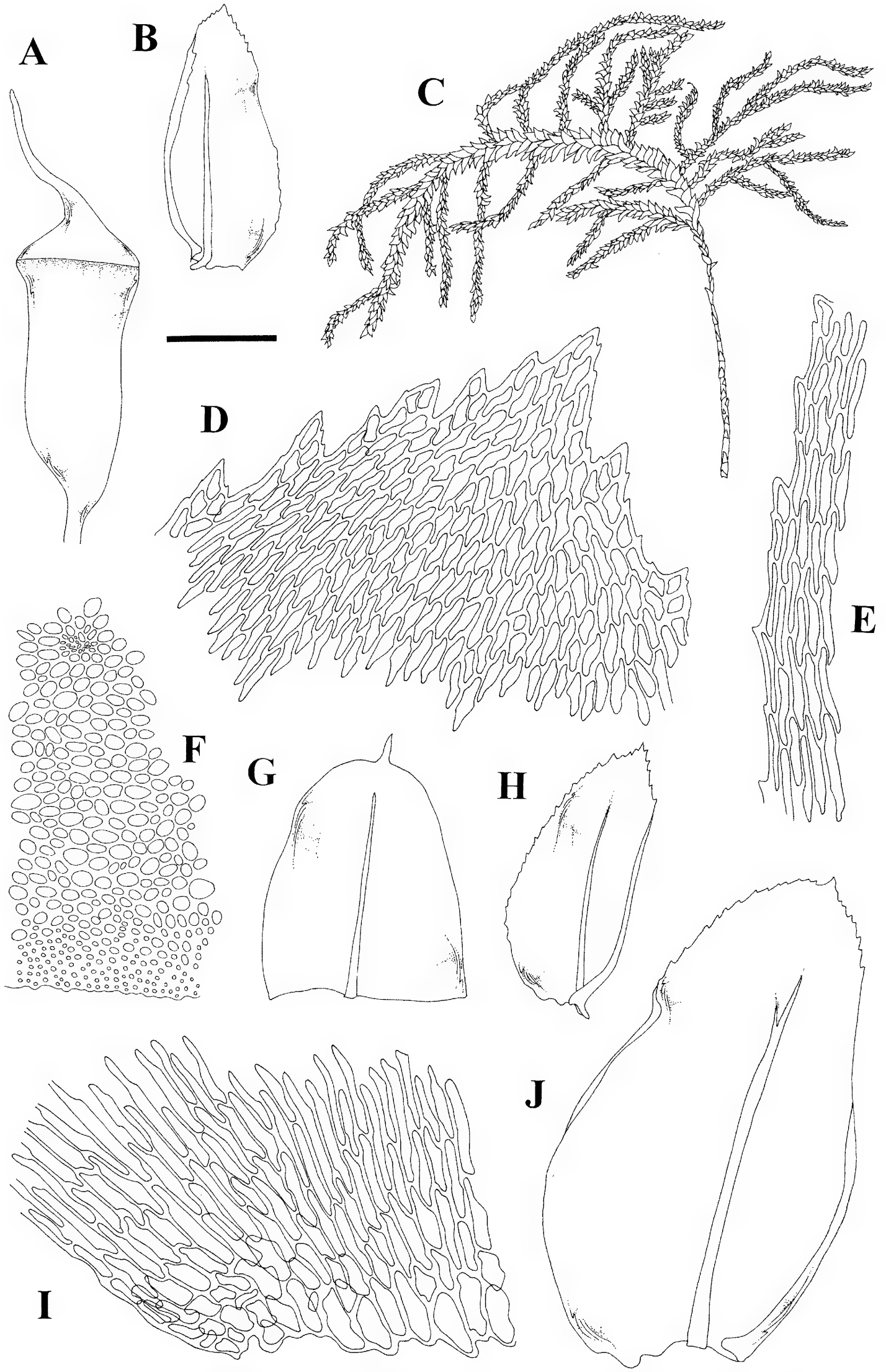


Figure 110. *Porotrichum lancifrons*. A. Seta, capsule, and operculum. B & H. Branch leaves. C. Habit. D. Leaf apex. E. Lower leaf cells and margin. F. Stem in cross section. G. Stipe leaf. I. Basal and alar cells. J. Stem leaf. Scale in mm: bar = 0.06 (D, E, I); bar = 0.13 (F); bar = 0.6 (B, G, H, J); bar = 1.25 (A); bar = 12.7 (C). A from *Davidse 28867*; all other figure parts from *Allen 12030*.

broad at base, tapering above, often spurred below, not or rarely weakly ending in a spine; cells smooth, upper cells rhomboidal to sigmoid-fusiform, 20–40 × 4–10 µm, median and basal cells elongate-fusiform to short-vermicular, 40–70 × 4–6 µm; alar cells subrectangular to subquadrate, thick-walled, porose, yellow red cells across the insertions porose; branch leaves flattened, spreading, oblong-ovate to elliptic or sometimes spathulate, 1.0–1.5 mm long; margins sharply serrate to dentate, teeth often multicellular and extending 3/4 of the way to the base, lower margins broadly inflexed on one side below, then shortly reflexed, otherwise similar to stem leaves. Dioicous. Setae 8–28 mm long, red to reddish brown, smooth. Capsules erect to inclined, ovoid-cylindrical, 2–3 mm long; exothecial cells small and thick-walled at mouth, rounded-rectangular to elongate-rectangular below, firm-walled; stomata at base; opercula conic at base, obliquely long-rostrate above, 1.5–2.0 mm long; annuli rudimentary; peristome diplolepideous; exostome teeth narrowly triangular, dorsal surface cross-striate below and coarsely papillose above, trabeculae and median line thin below, thickened above, ventral surface with projecting trabeculae, lightly papillose; endostome lightly papillose, basal membranes high, segments keeled, broadly perforate, cilia 1–3, nodose. Spores spherical, papillose, 13–18 µm. Calyptra not seen.

Illustrations. Buck (1998, Pl. 50 1–10). Figure 110.

Habitat. On dry cliff faces, the banks of stream gullies, boulders in forests and near streams, and on bark of tree trunks, vines, and roots; 1400–3200 m.

Distribution in Central America. HONDURAS. Comayagua: *Allen 12313* (MO); Francisco Morazán: *Olson 84-52* (MO); Lempira: *Allen 12030* (MO); Ocotepeque: *Allen 14545* (MO); Santa Bárbara: *Allen 11640* (MO). COSTA RICA. Alajuela: *Crosby 10003* (MO); Cartago: *Crosby & Crosby 5711* (MO); Heredia: *Crosby & Crosby 5783* (CR, F, FH, MO, NY, US); Limón: *Davidse et al. 28867* (MO); Puntarenas: *Gómez et al. 21817* (MO); San José: *Crosby 9692* (MO). PANAMA. Bocas del Toro: *Gómez et al. 21804* (MO); Chiriquí: *Allen 9157* (MO); Veraguas: *Crosby 10224* (MO).

World range: Mexico; Central America; Caribbean; Western and Northern South America, Brazil.

Porotrichum lancifrons is the one of the largest species of *Porotrichum* in Central America. Its robustness is manifested in plant aspect, height, stipe length, and in the remarkably large diameter of the stipes. Buck (1998) observed that plants of *P. lancifrons* at times have stipes longer than the fronds. The stipe leaves of *P. lancifrons* are broadly ovate-triangular to triangular, well spaced on the stipes, with plane margins, and they vary from appressed to erect-spreading. Plants with appressed stipe leaves are very distinctive, but the feature cannot be solely relied on as a distinguishing feature because there are other Central American species of *Porotrichum* with appressed stipe leaves. The secondary stem and branch leaves of *P. lancifrons* are complanate when dry and often striate to plicate. The stem leaves are oblong-ovate, somewhat asymmetric, and broadly apiculate. The branch leaves of *P. lancifrons* vary from oblong-ovate to elliptic, or spathulate. Regardless of branch leaf shape, their upper margins are more sharply serrate to dentate than the stem leaves, with the teeth more often multicellular. The branch leaves and stem leaves at base are broadly incurved on one side, then abruptly and shortly recurved. This feature is also present in *P. longirostre* and *P. filiferum*.

Sastre (1987) attributed a remarkable amount of variation in setae length (5–30 mm) to *P. lancifrons*, and on this basis proposed numerous synonyms for the species. Central American collections of *P. lancifrons* show the entire range of setae length. Moreover, a Costa Rican collection (*Crosby 10926*, MO) has plants with both extremes of setae length. Under a dissecting microscope the plants from this collection with different setae length have different aspects, but under the compound microscope they appear more or less the same. *Porotrichum lancifrons* has a hypnoid-type peristome with narrowly triangular exostome teeth that are strongly cross-striate on the lower dorsal surface and an endostome with a high basal membrane, well-developed, broadly keeled segments, and 1–3 nodose cilia. On the basis of its well-developed, hypnoid peristome this species has been treated as a *Porothamnium*.

In Central America only *P. longirostre* is likely to be confused with *P. lancifrons*. Both species have similar secondary stem and branch leaves that are sharply serrate to dentate to well below the middle of the leaves and have recurved basal margins. Plants of *P. longirostre*, however, are somewhat more slender than those of *P. lancifrons*, and its leaves are flexuose when dry rather than complanate.

Furthermore, the stem leaves in *P. longirostre* are never more than 2.5 mm long, while in *P. lancifrons* at least some stem leaves can be found that are over 3.0 mm long.

The type collection of *Porotrichum crassipes* is very scant; it consists of two capsules and the ultimate part of the stem along with several branches. The type collector is Tonduz and not, as seems to be indicated by the protologue, Pittier. The protologue citation "(*Pitt. n° 5652*)" refers to its number in H. Pittier and Th. Durand's *Plantae costaricenses exsiccatae*.

6. *Porotrichum longirostre* (Hook.) Mitt., J. Linn. Soc., Bot. 12: 461. 1869. *Neckera longirostris* Hook., Musc. Exot. 1: 1. 1818. *Climacium longirostre* (Hook.) Brid., Bryol. Univ. 2: 275. 1827. *Hypnum porotrichum* Müll. Hal., Syn. Musc. Frond. 2: 223. 1851, new name in *Hypnum*, not *Hypnum longirostrum* Erhr. *ex* Brid., 1801. *Porophyllum longirostrum* (Hook.) Schimp. *ex* Paris, Index Bryol. 1015. 1898, invalid name, listed in synonymy. *Thamnium longirostre* (Hook.) Kindb., Hedwigia 41: 232. 1902. Protologue. Hab. regione temperata, in jugis Andium. *Humboldt et Bonpland.* Type. Hab. Regione temperata. Jugis Andinum, *Humboldt & Bonpland* (NY, isotype).

Porotrichum mexicanum Schimp. *ex* Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 246. 1872. *Thamnium mexicanum* (Schimp. *ex* Besch.) Kindb., Hedwigia 41: 234. 1902. Protologue. [Mexico] Orizaba (*F. Müller* in herb. Schimper). Type. Orizaba, Mexico, coll. *Fr. Müller* (MO, isotype).

Porotrichum plagiorhynchum Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32(1): 45. 1894. *Thamnium plagiorhynchum* (Renauld & Cardot) Kindb., Hedwigia 41: 233. 1902. Protologue. [Costa Rica] Forêts du Barba, 2500–2800 m, (*Pitt.*[*ier*] *n^os 5644, 5724*) et de l'Irazu (*n^os 5645-5647*). Types. Costa Rica. H. Pittier & Th. Durand Plantae costaricenses exsiccatae, Forêts du Barba, 2700–2800 m, 6-II-1890, legit [H. Pittier] *Biolley N° 5644* (US, syntype); Costa Rica. H. Pittier & Th. Durand Plantae costaricenses exsiccatae, Forêts de l'Irazu, 10-7-1891, legit [H. Pittier] *Tonduz 5645*, *5646*, *5647* (all US, syntypes); Costa Rica forets de l'Irazu, leg. *Tonduz*, 1891 (FH, syntypes).

Plants medium-sized to robust, to 10 cm high, stipitate-frondose, stipe sometimes as long or longer than the frond, forming green to pale green, glossy, lax tufts. Stolons creeping, densely and thickly tomentose, evenly foliate; rhizoids long, sparsely and irregularly branched, smooth to lightly roughened, red to reddish brown, in dense circular clusters just below the leaf insertions, on stolons, and at the base of stipitate stems; leaves appressed, widely spaced, ovate-triangular to triangular, 0.5–1.0 mm long. Stems erect, stipitate, irregularly 2–3-pinnate, complanate-foliate; stems in cross section with sclerodermis of 5–8 rows of small, thick-walled cells, grading into larger, thick-walled cortical cells, central strand well developed; paraphyllia absent; pseudoparaphyllia foliose. Stipes evenly foliate; leaves appressed or appressed below, erect-spreading above, 1.0–1.4 mm long at midstipe, broadly triangular, long-cuspidate; margins entire to subserrulate, plane; costae single, strong, 3/4 the leaf length, or weak and nearly absent. Stem leaves flattened, spreading, often striate-plicate when dry, 1.4–2.5 mm long, oblong-ovate, somewhat asymmetric, broadly acute, broadly apiculate; margins serrate or dentate at apex, teeth mostly 1-celled, sometimes of 2–3 cells, serrulate to midleaf or somewhat below midleaf; costae single, 2/3 the leaf length, broad at base, tapering above, at times spurred below, not or rarely weakly ending in a spine; cells smooth, upper cells rhomboidal to sigmoid-fusiform, 18–28 × 6–8 µm, median and basal cells elongate-fusiform to short-vermicular, 18–70 × 4–6 µm; alar cells subrectangular to subquadrate, thick-walled, porose, cells across the insertions porose and yellow red. Branch leaves crispate when dry, oblong-ovate, oblong-obovate, or elliptic or sometimes spathulate, 1.0–1.5 mm long; margins sharply serrate to dentate, teeth often multicellular, lower margin broadly inflexed on one side below, then shortly reflexed, otherwise similar to stem leaves. Dioicous. Setae 20–30 mm long, red to reddish brown, smooth. Capsules erect to inclined, ovoid-cylindrical, 2–2.5 mm long; exothecial cells small and thick-walled at mouth, rectangular to elongate-rectangular below, firm-walled, cells in neck irregularly isodiametric, thick-walled; stomata on neck; opercula conic at base, obliquely long-rostrate above, 2.0–2.5 mm long; annuli well developed, deciduous but not revoluble; peristome diplolepideous; exostome teeth narrowly triangular, dorsal surface densely cross-striate below and coarsely papillose above, trabeculae and median line thin below, thickened above, ventral surface with trabeculae thickened above, densely papillose; endostome papillose, basal membranes high, segments keeled, broadly perforate, cilia rudimentary, 1–3. Spores spherical to oval, thickly papillose, 12–22 µm. Calyptrae cucullate, yellow, smooth, naked, to 4 mm long.

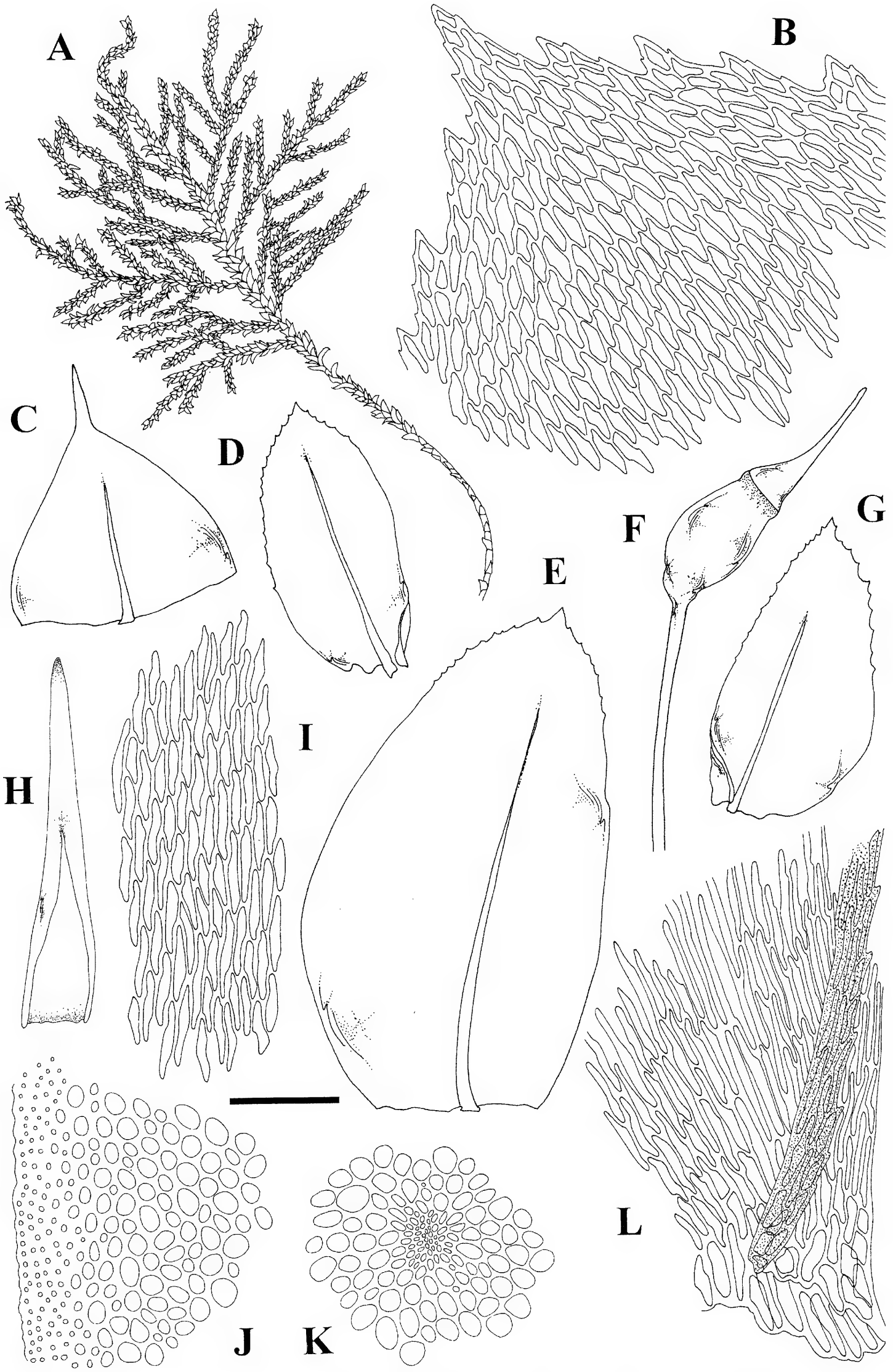
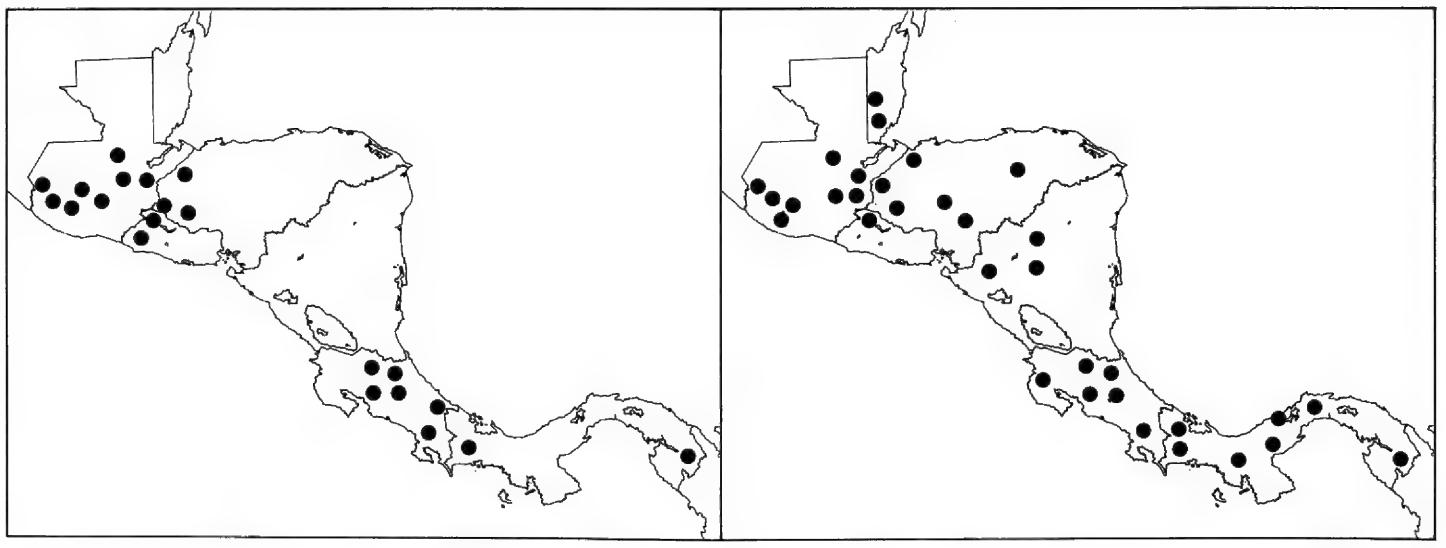


Figure 111. *Porotrichum longirostre*. A. Habit. B. Leaf apex. C. Stipe leaf. D & G. Branch leaves. E. Stem leaf. F. Seta, capsule, and operculum. H. Calyptra. I. Median leaf cells. J & K. Stem in cross section. L. Basal and alar cells. Scale in mm: bar = 0.06 (B, I, L); bar = 0.08 (J, K); bar = 0.5 (C–E, G); bar = 0.7 (H); bar = 1.56 (F); bar = 10.1 (A). F from *Hammel 18327*; H from *Gómez 18865*; all other figure parts from *Allen 11415*.



Porotrichum longirostre *Porotrichum mutabile*

Illustrations. Hooker (1818, Tab. 1); Sharp *et al.* (1994, Figs. 565 & 566); Buck (1998, Pl. 48 10–18). Figure 111.

Habitat. On bark of tree trunks and branches, rotting logs, terrestrial on moist soil, and occasionally on boulders by streams; 1250–3109 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: *Standley 91409* (F, FH); Chimaltenango: *Standley 60034* (F, FH); El Progreso: *Steyermark 43580* (F, FH, US); Guatemala: *Standley 58415a* (F, FH); Quetzaltenango: *Standley 85051* (F, FH); San Marcos: *Standley 68649* (F, FH, MO); Sololá: *Steyermark 47568* (F, FH, MO, US); Zacapa: *Steyermark 43580* (F, FH, US). EL SALVADOR. Santa Ana: *Watson ES-0090* (MO); Sonsonate: *Winkler 10* (MO). HONDURAS. Lempira: *Allen 11415* (MO); Santa Barbára: *Allen 11633* (MO); Ocotepeque: *Allen 14427* (MO). COSTA RICA. Alajuela: *Crosby 9970* (MO); Cartago: *Maxon & Harvey 8177* (NY, US); Heredia: *Crosby 9885* (MO); Limón: *Davidse et al. 26091* (CR, MO, NY); Puntarenas: *Lyon 423* (MO); San José: *Standley 38776* (FH, MO, US). PANAMA. Chiriquí: *Martin 4310* (FH, NY); Darién: *Folsom 4471* (MO).

World range: Mexico; Central America; Caribbean; Western and Northern South America, Brazil.

Porotrichum longirostre is a medium-sized to robust species that usually occurs on trees and branches rather than rocks and can be as large as *P. lancifrons*. As in that species, the stipes of *P. longirostre* have well-developed central strands and can be longer than the fronds. The stipe leaves of *P. longirostre* are broadly triangular, well spaced on the stipes, with plane margins, and they vary from appressed to erect-spreading. The stem leaves of *P. longirostre* are complanate, oblong-ovate, somewhat asymmetric, broadly acute to broadly apiculate, and often striate to plicate when dry. The branch leaves of *P. longirostre* are distinctively crispate rather than flattened when dry, and oblong-ovate, oblong-obovate, elliptic, or sometimes spathulate. The branch leaves, and often those on the stems, are broadly incurved below on one side, then abruptly and shortly recurved. This very distinctive branch leaf feature serves to distinguish it from all other Central American species of *Porotrichum* except *P. lancifrons* and *P. filiferum*. *Porotrichum longirostre* has long setae and a hypnoid-type peristome: exostome teeth narrowly triangular, strongly cross-striate on the lower dorsal surface; endostome basal membrane high, segments broadly perforate and keeled, cilia 1–3, but rudimentary.

In Central America *P. longirostre* is more likely to be confused with *P. lancifrons* than any other species. These species both have branch leaves that are sharply serrate to dentate to well below the middle of the leaves; they also have shortly recurved basal leaf margins. Plants of *P. lancifrons*, however, are usually more robust than those of *P. longirostre* and its branch leaves are complanate-flattened rather than flexuose when dry. Furthermore, the largest stem leaves in *P. lancifrons* are over 3.0 mm long, while in *P. longirostre* they are never more than 2.5 mm long. As noted above, *P. filiferum* is similar to *P. longirostre* in having branch leaves with recurved basal margins. It is usually, however, a smaller species than *P. longirostre*, and its leaves are flattened rather than flexuose when dry. Furthermore, the stipe leaves of *P. filiferum* differ reliably from those of *P. longirostre* in having broadly incurved margins.

Allen (1994) tentatively placed *P. mutabile*, *P. insularum*, and *P. plagiorhynchum* in the synonymy of *P. longirostre*. *Porotrichum plagiorhynchum* is indeed a synonym of *P. longirostre*; however, *P. mutabile* (with *P. insularum* as a synonym) is a distinct species. Large forms of *P. mutabile* are similar to small forms of *P. longirostre* in size, and *P. mutabile* often has more or less equally foliate ultimate branch leaves that give it an aspect somewhat similar to that of *P. longirostre*. Although the branch and stem leaves of *P. mutabile* are incredibly variable in form, making it hard to characterize the species, they consistently differ from those of *P. longirostre* in having plane basal margins. The illustrations of *P. longirostre* in Bartram (1949) appear to represent *P. mutabile*.

7. *Porotrichum mutabile* Hampe, Flora 45: 456. 1862, new name for *Neckera flabellata* Hampe, Linnaea 31: 525. 1862, illegitimate homonym, not *Neckera flabellata* (Sm.) Mitt., 1859. Protologue. [Colombia] Nova-Granada, Cipacon in sylv., alt. 2600 metr., Aug. 1861, sub [*Lindig*] no. *2095*.

Porotrichum variabile Hampe, Ann. Sci. Nat., Bot. sér. 5, 4: 375. 1865, illegitimate name, includes type of earlier name. *Thamnium variabile* (Hampe) Kindb., Hedwigia 41: 233. 1902, illegitimate name. Protologue. [Colombia] Bogotá, Tequendama, Canoas et Choachi, 2500–2600 m, in sylv. ad arb. sub n° *2095* leg. *A. Lindig.*

Porotrichum insularum Mitt., J. Linn. Soc., Bot. 12: 464. 1869. Protologue. Hab. Ins. Dominica, *M'Imray*; Martinique, ex Herb. Schimper; Guadelupe, *Perrottet*. Type. Dominica, *M'Imray* (MO, isotype).

Porotrichum pringlei Cardot, Rev. Bryol. 37: 8. 1910. Protologue. [Mexico] État de Vera Cruz: près de Jalapa, 1908 (*Pringle, n. 15151 in parte*). Types. Mexico. Vera Cruz near Jalapa, June 24, 1908, *C. G. Pringle 15151* (MO, US, isotypes).

Plants medium-sized, 3–8 cm high, stipitate-frondose, forming pale green to yellow green, lax, at times wiry, tufts. Stolons creeping, evenly foliate; rhizoids smooth to lightly roughened, red to reddish brown, sparsely and irregularly branched, in dense circular clusters just below the leaf insertions, on stolons, and at the base of stipitate stems; leaves appressed, widely spaced, 0.3–0.5 mm long, ovate-triangular to triangular. Stems erect, stipitate, irregularly 2–3-pinnate, complanate-foliate; stems in cross section with sclerodermis of 5–6 rows of small, thick-walled cells, grading into larger, firm- or thick-walled cortical cells, central strand present; paraphyllia absent; pseudoparaphyllia foliose. Stipes evenly foliate; leaves appressed below, erect-spreading above, becoming progressively larger from the base to the first branch, 0.8–1.2 mm long at mid-stipe, ovate-triangular to triangular, acute to acuminate; margins entire to subserrulate, plane; costae strong, 3/4 the leaf length. Stem leaves flattened, spreading, often striate-plicate when dry, 2.0–3.0 mm long, ovate to oblong-ovate, somewhat asymmetric, broadly acute or short-acuminate; margins serrate or dentate at apex, teeth mostly 1-celled, sometimes of 2–3 cells, serrulate to well below midleaf, broadly incurved below on one side; costae single (occasionally double), 2/3 the leaf length, broad at base, tapering above, often spurred below, not or rarely weakly ending in a spine; cells smooth, upper cells rhomboidal, 14–30 × 6–10 µm, median and basal cells elongate-fusiform to short-vermicular, 30–90 × 4–6 µm; alar cells subrectangular to subquadrate, thick-walled, porose, cells across the insertions porose and yellow red. Branch leaves erect-spreading to spreading, often flattened, extremely variable in shape: ovate, oblong-ovate, oblong-ligulate, or ligulate, occasionally spathulate, 0.7–1.5 mm long, acute; margins sharply serrate to dentate above, teeth often multicellular, lower margin broadly inflexed on one side below; upper cells of ultimate branch leaves elongate-flexuose and porose, otherwise similar to stem leaves. Asexual reproduction by deciduous, flagellate branch tips, flagellate branches in leaf axils, or deciduous leaves. Dioicous. Setae short, 3–10 mm long, red to reddish brown, smooth to lightly roughened. Capsules erect to inclined, broadly cylindrical to cylindrical, 1–2 mm long; exothecial cells small and thick-walled at mouth, rounded-rectangular to rectangular below, firm- to thick-walled; stomata at base of capsules; opercula conic at base, obliquely long-rostrate above, 1.0–1.5 mm long; annuli rudimentary; peristome diplolepideous; exostome teeth narrowly triangular, reddish below, pale yellow above, dorsal surface cross-striate below and coarsely papillose above, trabeculae and median line thin below, thickened above, ventral surface with projecting trabeculae, lightly papillose; endostome pale yellow, densely papillose, basal membranes high, segments linear, not keeled, perforate, often united at tips, cilia absent or rudimentary. Spores spherical, lightly papillose, 12–18 µm. Calyptrae 1.5–2.0 mm long, yellow, cucullate, smooth, naked.

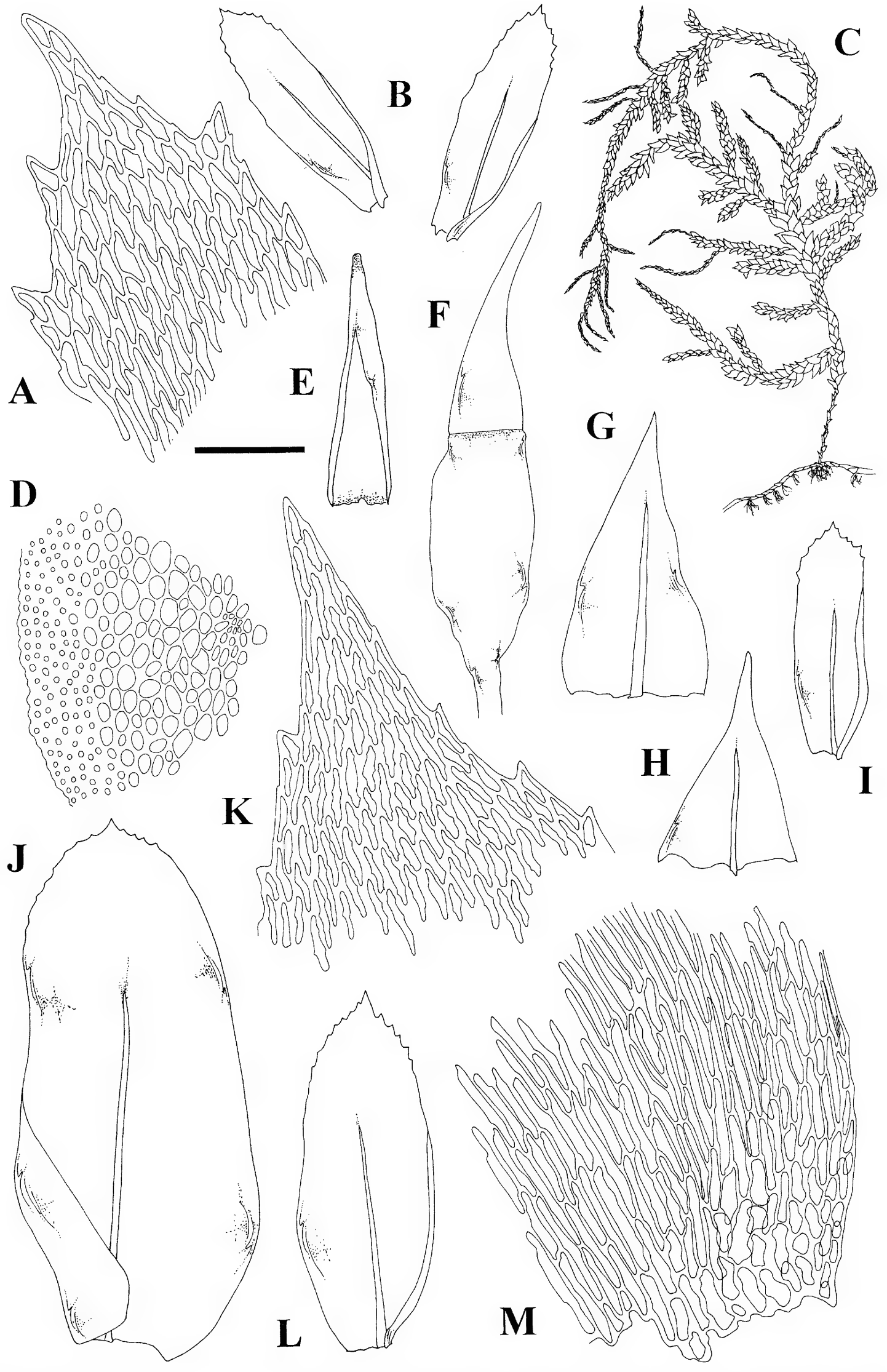


Figure 112. *Porotrichum mutabile*. A. Ultimate branch leaf apex. B, I & L. Branch leaves. C. Habit. D. Stem in cross section. E. Calyptra. F. Seta, capsule, and operculum. G & H. Stipe leaves. J. Stem leaf. K. Leaf apex. M. Basal and alar cells. Scale in mm: bar = 0.06 (A, K, M); bar = 0.08 (D); bar = 0.5 (B, G–J, L); bar = 0.7 (E); bar = 0.9 (F); bar = 8.0 (C). E from *Crosby 10211*; all other figure parts from *Allen 12389*.

Illustrations. Bartram (1949, Fig. 127 H–J, as *Porotrichum longirostre*); Sharp *et al.* (1994, Fig. 564 e–k); Churchill and Linares (1995, Fig. 191 a–g); Duarte Bello (1997, Pl. 217); Buck (1998, Pl. 48 1–9); Gradstein *et al.* (2001, Fig. 217 G–M). Figure 112.

Habitat. On bark, tree trunks, branches, twigs, vines, and logs, on soil, at times pendent, occasionally on boulders along streams; 400–2480 m.

Distribution in Central America. BELIZE. Cayo: *Allen 15077* (MO); Toledo: *Allen 18632* (BRH, MO). GUATEMALA. Alta Verapaz: *Standley 71605* (F, FH); Chiquimula: *Steyermark 30782* (F, FH, MO); Jalapa: *Steyermark 32368* (F, FH); Quetzaltenango: *Standley 65390* (F, FH); San Marcos: *Standley 68556a* (F, FH, MO); Sololá: *Steyermark 47249* (F, FH); Suchitepéquez: *Steyermark 46661b* (F, FH); Zacapa: *Steyermark 29927* (F). EL SALVADOR. Santa Ana: *Davidse et al. 37327* (MO). HONDURAS. Copán: *Allen 17767* (MO, TEFH); Cortés: *Allen 14190* (MO); Comayagua: *Allen 13977* (MO, TEFH); Francisco Morazán: *Allen 12389* (MO); Lempira: *Allen 11372* (MO, TEFH); Olancho: *Allen 12830C* (MO). NICARAGUA. Estelí: *Moreno 19246A* (MO, NY); Jinotega: *Standley 10984* (F, FH); Matagalpa: *Richards et al. 3761* (F, MO). COSTA RICA. Alajuela: *Crosby & Crosby 6093* (MO); Cartago: *Gómez 19756* (MO); Guanacaste: *Dauphin 2583* (MO); Heredia: *Standley 51509* (FH, US); Puntarenas: *Lyon 191* (MO); San José: *Standley 38092* (FH, US). PANAMA. Bocas del Toro: *Allen 5708* (MO, PMA); Chiriquí: *Allen 5347* (MO, PMA); Coclé: *Crosby 4397* (MO); Colón: *Crosby 10356* (MO); Darién: *Allen 8888* (MO, PMA); Panamá: *Crosby 10075* (MO); Veraguas: *Crosby 10211* (MO).

World range: Mexico; Central America; Caribbean; Northern and Western South America, Brazil.

Porotrichum mutabile is the most common *Porotrichum* species in Central America, where it typically grows on trees, branches, vines, or logs. Only occasionally is it found on rocks. It is a medium-sized, pale green to yellow green species, with erect to erect-spreading stipe leaves that have plane margins. The stem leaves are ovate to oblong-ovate, typically complanate, and broadly rounded at the apex, while the primary and secondary branch leaves are incredibly variable in stance and form. In large collections both complanate and evenly foliate branch leaves can be found: sometimes they occur on single plants. At the same time single collections can have ovate, oblong-ovate, oblong-ligulate, ligulate, or spathulate branch leaves. For this reason branch leaf shape cannot be used to distinguish *P. mutabile* from many other *Porotrichum* species.

The secondary stem and branch leaves of *P. mutabile* nearly always have one margin broadly incurved at base; otherwise the margins are plane. Typically, the apical stem and branch leaf cells are rhomboidal and smooth; however, the ultimate branch leaf apices have long, flexuose, porose cells. Collections of *P. mutabile* nearly always have deciduous, flagellate branch tips or flagellate branches in leaf axils. Some collections consist nearly entirely of these flagellate branches. *Porotrichum mutabile* differs from all other Central American species of *Porotrichum* in having short (3–10 mm) setae.

Porotrichum longirostre is similar to *P. mutabile* in size and in having erect-spreading to spreading, plane-margined stipe leaves. It differs in having leaves that are crispate when dry, and it often has longer stipes. The best features for distinguishing the two species, however, are found in the branch leaves. In *P. longirostre* the branch leaves are fairly consistently elliptic and (as in *P. mutabile*) are broadly inflexed below on one side, but then the margins are narrowly recurved on one or both sides. This feature is apparent under microscopic examination of both attached and detached leaves, and causes the leaves to be "strikingly narrower at the insertion" (Buck 1998). The branch leaves of *P. longirostre* also differ from those of *P. mutabile* in having shorter, non-porose apical cells. In Central America *P. longirostre* often has sporophytes that are considerably longer (20–30 mm vs. 3–10 mm) than those of *P. mutabile*.

Porotrichum korthalsianum usually differs from *P. mutabile* in its dark green color, weakly to unbranched stems, consistently complanate branch leaves, and general lack of deciduous flagelliform branches. Furthermore, it has an aspect more similar to *Thamnobryum* than most other species of *Porotrichum.* The two species, however, are similar in size, have identical stipe leaves, more or less similar stem leaves, and branch leaves that are broadly incurved below on one side, but otherwise plane. *Porotrichum korthalsianum* differs from *P. mutabile* in having consistently broader branch leaves that are always broadly rounded at the apex and have rhomboidal, non-porose apical cells. The presence in *P. mutabile* of incredibly variable branch leaves is bound to result in some difficulty in separating the two species. In this regard it is important to always examine the ultimate branch leaves.

8. *Porotrichum pittieri* Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32(1): 188. 1894. *Thamnium pittieri* (Renauld & Cardot) Kindb., Hedwigia 41: 242. 1902. Protologue. [Costa Rica] Forêts de l'Irazu (*Pitt*[*ier*] *n*^{o} *5648*). Forêts du Rio-Naranjo, échantillon stérile et douteux ([*Pittier*] *n*^{o} *5704*). Type. H. Pittier & Th. Durand, *Plantae costaricenses exsiccatae N*^{o} *5648*, Forêts de l'Irazu 10-VII-1891, legit H. Pittier. *Tonduz* (US, lectotype, designated here).

Plants medium-sized, 3–6 cm high, stipitate-frondose, forming pale green to yellow green, lax tufts. Stolons creeping, evenly foliate; rhizoids smooth to lightly roughened, red to reddish brown, sparsely and irregularly branched, in dense circular clusters just below the leaf insertions, on stolons, and at the base of stipitate stems; leaves appressed, widely spaced, 0.3–0.5 mm long, ovate-triangular to triangular. Stems erect, stipitate, irregularly 2–3-pinnate, complanate-foliate; stems in cross section with sclerodermis of 5–6 rows of small, thick-walled cells, grading into larger, thick-walled cortical cells, central strand present; paraphyllia absent; pseudoparaphyllia foliose. Stipes evenly foliate; leaves appressed below, erect-spreading to spreading above, becoming progressively larger from the base to the first branch, 0.8–1.2 mm long at mid-stipe, ovate-triangular to triangular, acute to acuminate; margins entire to subserrulate, plane; costae strong, 3/4 the leaf length. Stem leaves 2.0–3.0 mm long, flattened, spreading, often striate-plicate when dry, oblong-ovate, somewhat asymmetric, broadly acute or short-acuminate; margins serrate or dentate at apex, teeth mostly 1-celled, serrulate to well below midleaf, broadly incurved below on one side; costae single (occasionally double), 1/2–2/3 the leaf length, broad at base, tapering above, sometimes spurred below, not ending in a spine; cells smooth, upper cells rhomboidal, 14–28 × 6–10 µm, median and basal cells elongate-fusiform to short-vermicular, 30–90 × 4–6 µm; alar cells subrectangular to subquadrate, thick-walled, porose, yellow red, cells across the insertions porose and yellow. Branch leaves erect-spreading to spreading, often flattened, 0.7–1.5 mm long, oblong-ovate, oblong-ligulate, or ligulate, acute; margins sharply serrate to dentate above, teeth often multicellular, lower margin broadly inflexed on one side below; upper cells of ultimate branch leaves elongate-flexuose and porose, otherwise similar to stem leaves. Asexual reproduction by deciduous, flagellate branch tips, flagellate branches in leaf axils, or deciduous leaves. Dioicous. Setae 15–25 mm long, red to reddish brown, smooth. Capsules erect to inclined, broadly cylindrical to cylindrical, constricted at the neck, 1.5–2.0 mm long; exothecial cells small and thick-walled at mouth, rounded-rectangular to rectangular below, firm-walled; stomata at base of capsules; opercula conic at base, obliquely long-rostrate above, 2.0–2.5 mm long; annuli rudimentary; peristome diplolepideous; exostome teeth linear, yellow below, pale yellow above, dorsal surface papillose and cross-striate in lower 1/2, and densely papillose above, trabeculae and median line thin, ventral surface with projecting trabeculae, lightly papillose; endostome pale yellow, densely papillose, basal membranes high, segments linear, not keeled, broadly perforate, cilia 1–2, rudimentary. Spores spherical, lightly papillose, 14–18 µm. Calyptrae 3.5 mm long, yellow, cucullate, smooth, naked.

Illustration. Figure 113.

Habitat. On tree trunks; 1100–2350 m.

Distribution in Central America. HONDURAS. Comayagua: *Allen 13980* (MO); Lempira: *Allen 11359* (MO); Olancho: *Allen 12591* (MO). COSTA RICA. Cartago: *Tonduz* (US); San José: *Holz 340* (NY).

World range: Central America.

Porotrichum pittieri is a medium-sized species with well-branched stems and weakly developed costae, but otherwise gametophytically identical to *P. mutabile. Porotrichum mutabile* is gametophytically extremely variable, and for that reason the distinctive gametophytic features of *P. pittieri* noted above will not adequately distinguish the two species. *Porotrichum mutabile* differs from *P. pittieri* in its shorter setae (3–10 mm vs. 15–25 mm), opercula (1.0–1.5 mm vs. 2.0–2.5 mm), and calyptrae (1.5–2.0 mm vs. 3.5 mm).

9. *Porotrichum substriatum* (Hampe) Mitt., J. Linn. Soc., Bot. 12: 463. 1869. *Neckera substriata* Hampe, Ann. Sci. Nat., Bot., sér. 5, 5: 340. 1866. *Thamnium substriatum* (Hampe) Kindb., Hedwigia 41: 227. 1902. *Porothamnium substriatum* (Hampe) M. Fleisch. *ex* Broth., Nat. Pflanzen-

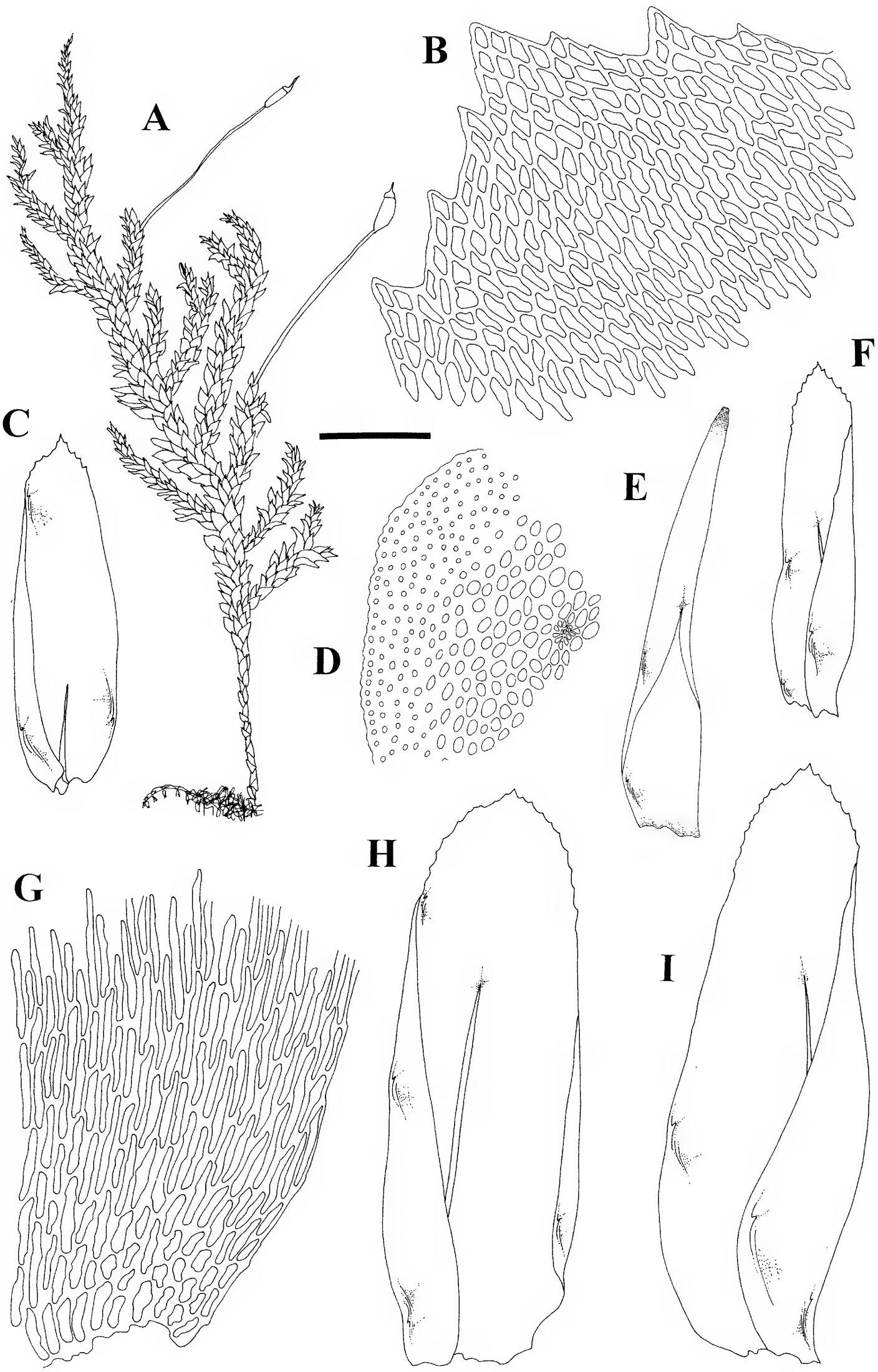
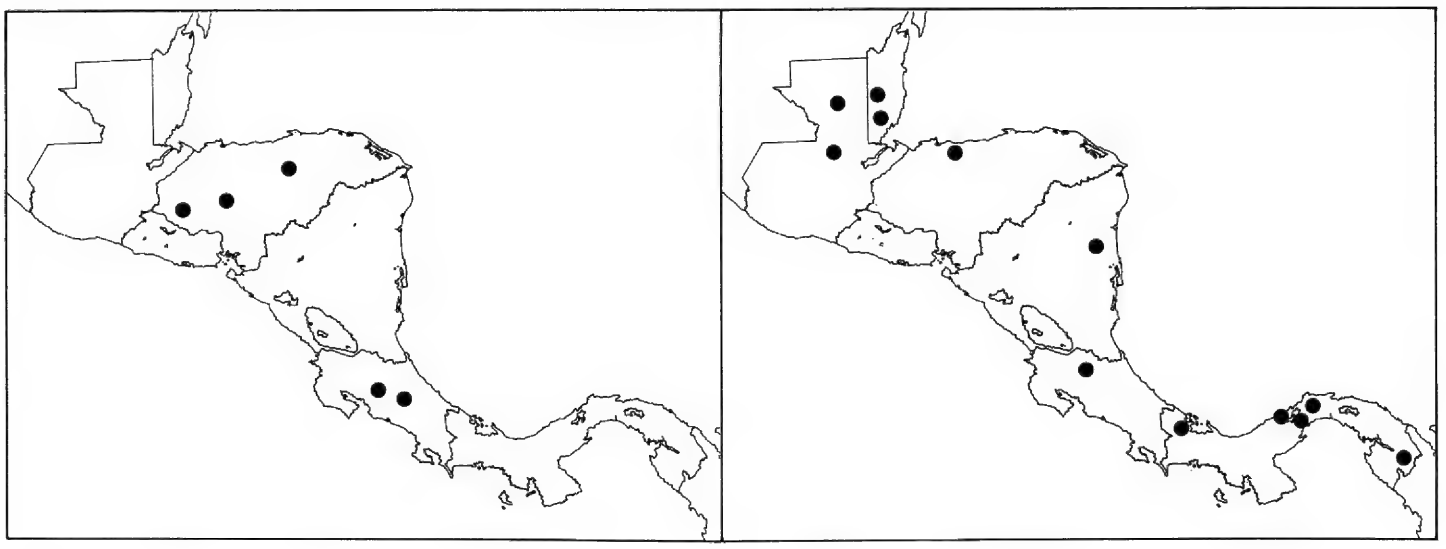


Figure 113. *Porotrichum pittieri*. A. Habit. B. Leaf apex. C & F. Branch leaves. D. Stem in cross section. E. Calyptra. G. Basal and alar cells. H & I. Stem leaves. Scale in mm: bar = 0.06 (B, G); bar = 0.08 (D); bar = 0.5 (C, F, H, I); bar = 0.8 (E); bar = 7.2 (A). E from *Allen 13980*; all other figure parts from *Pittier 5648* (type).



Porotrichum pittieri *Porotrichum substriatum*

fam. (ed. 2) 11: 199. 1925. Protologue. [Colombia] Hab. Bogotá, San-Antonio, 1400 metr., pauca specimina sterilia intermixta legit *A. Lindig*.

Porotrichum plicatulum Mitt., J. Linn. Soc., Bot. 12: 461. 1869. *Thamnium plicatulum* (Mitt.) Kindb., Hedwigia 41: 253. 1902, illegitimate homonym, not *Thamnium plicatulum* Sande Lac., 1866. Protologue. Hab. Ins. Trinidad, in sylvis Arima, *Purdie*; Chaguanas, *Black*. Type. Trinidad, *Dr. Black 92* (MO, syntype).

Pireella squarrosa Arzeni, Amer. Midl. Naturalist 52: 33. 1954. *Porotrichum squarrosum* (Arzeni) H. A. Crum & Steere, Amer. Midl. Naturalist 60: 33. 1959. Protologue. Haiti: Hardwood patch en route Savanne Zombi, Mornes des Commissaires, Apr. 28, 1944, *Faith P. Mackaness 99*. Type. Haiti, Mornes des Commissaires, *Mackaness 99* (MO, isotype).

Plants small to somewhat medium-sized, 1–3(–5) cm high, stipitate-frondose, forming pale green to dark green, lax tufts. Stolons creeping, evenly foliate; rhizoids smooth to lightly roughened, red to reddish brown, not or sparsely branched, in circular clusters just below the leaf insertions, on stolons, and at the base of stipitate stems; leaves imbricate, widely spaced, 0.3–0.6 mm long, triangular, ecostate. Stems erect, stipitate, 1-pinnate, frondose, evenly foliate to strongly complanate, at times flagellate-attenuate; stems in cross section with sclerodermis of 4–6 rows of small, thick-walled cells, grading into larger, firm-walled cortical cells, central strand present; paraphyllia absent; pseudoparaphyllia subfoliose to nearly filiform. Stipes evenly foliate; leaves appressed below, squarrose-recurved to recurved above, 0.6–1.0 mm long, ovate-triangular to triangular, acute to acuminate; margins entire to subserrulate, broadly recurved below; costae single and strong, ending 1/2–2/3 the leaf length. Stem leaves more or less plicate to striate when dry, erect-spreading when wet, 1–2 mm long, ovate-lanceolate, ovate, or oblong-ovate, more or less symmetric, short-acuminate to cuspidate, shortly decurrent; margins serrate to serrulate above, serrulate to subentire below, more or less inflexed below on one side, plane or narrowly recurved on the other; costae single, at times spurred below, tapering at the ends, often stoutly projecting at tips, 2/3–3/4 the leaf length; cells smooth or prorate, upper cells fusiform to elongate-fusiform, 20–40 × 4–6 µm, median cells elongate-fusiform to elongate, 30–40 × 4–6 µm; basal cells elongate-linear, cells at the extreme base porose; alar cells weakly differentiated as a few oblate, quadrate, or short-rectangular cells at the basal angles, cells across the insertions yellow. Branch leaves wide-spreading, variously flattened, similar to stem leaves except smaller. Asexual reproduction by axillary, microphyllous, flagelliform branches. Dioicous. Perichaetia lateral on stems and branches, 0.5–1.0 mm long; leaves convolute at base, spreading above, abruptly long-acuminate, margins subentire, costae absent. Sporophytes unknown.

Illustrations. Bartram (1949, Fig. 127 D–G); Arzeni (1954, Pl. 20); Crum and Steere (1958, Figs. 62–83); Florschütz-de Waard (1986, Fig. 110); Sharp *et al.* (1994, Fig. 564); Buck (1998, Pl. 47); Buck (2003, Fig. 109). Figure 114.

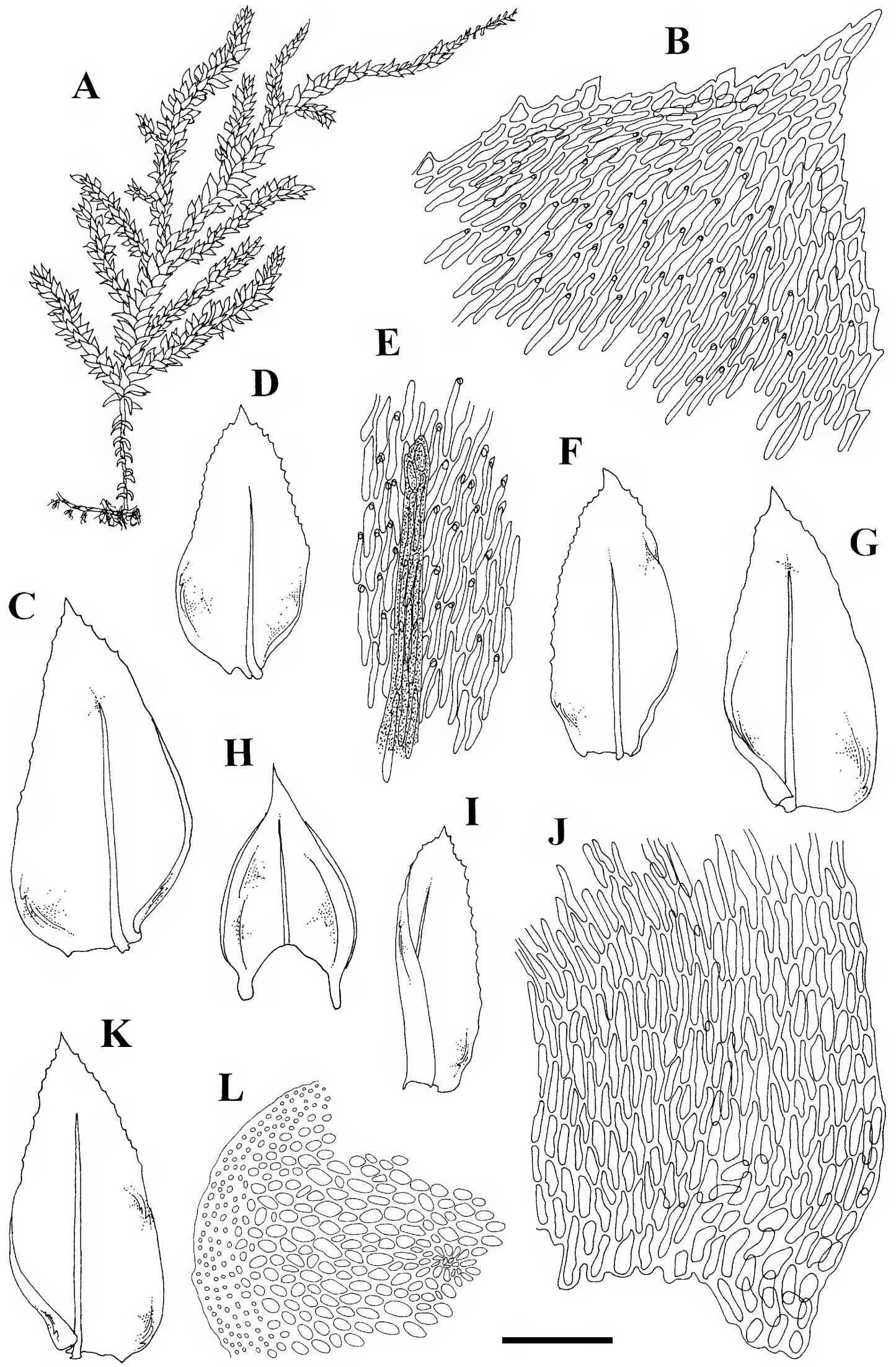


Figure 114. *Porotrichum substriatum*. A. Habit. B. Leaf apex. C, G & K. Stem leaves. D, F & I. Branch leaves. E. Upper leaf cells and tip of costa. H. Stipe leaf. J. Basal and alar cells. L. Stem in cross section. Scale in mm: bar = 0.05 (B, E, J); bar = 0.08 (L); bar = 0.4 (C, D, F–I, K); bar = 5.4 (A). All figure parts from *Allen 17242*.

Habitat. On rocks and boulders in woods, tree trunks, roots, lianas, twigs, and rotting logs; 20–1000 m.

Distribution in Central America. BELIZE. Cayo: *Allen 15518B* (MO); Toledo: *Croat 24164* (MO). GUATEMALA. Alta Verapaz: *Steyermark 44426* (F, FH); Petén: *Lundell 2699* (FH). HONDURAS. Atlántida: *Allen 17578* (MO, TEFH). NICARAGUA. Zelaya: *Stevens 13072* (MO). COSTA RICA. Alajuela: *Standley 40142* (FH, MO, US). PANAMA. Bocas del Toro: *Allen 5614* (MO); Canal Area: *Steyermark & Allen 17165* (MO); Colón: *Crosby 10321* (MO); Darién: *Allen 8743* (MO); Panamá: *Crosby 4335* (MO).

World range: Mexico; Central America; Caribbean; Western and Northern South America, Brazil; West, Northeast, West-Central, and East Tropical Africa.

Porotrichum substriatum is a small to medium-sized plant with distinctly squarrose recurved stipe leaves that have broadly recurved basal margins. The secondary stem and branch leaves are plicate when dry, more or less evenly foliate, and often ovate-lanceolate. Although the leaf costae taper to the tips, they are strong throughout and almost always end in a stout spine. The leaf cells typically are strongly prorate. *Porotrichum substriatum* differs from all other Central American members of *Porotrichum* in having squarrose-recurved stipe leaves and evenly foliate, ovate-lanceolate leaves that having stoutly spined costae and prorate leaf cells. *Porotrichum filiferum* is similar to *P. substriatum* in size and in having stipe leaves with broadly recurved margins. It differs from *P. substriatum* in having spreading to reflexed stipe leaves, as well as stem and branch leaves that have a narrow costa that rarely projects as a spine, smooth leaf cells, and basal margins that are broadly inflexed then narrowly recurved on one side.

There is a form of *Porotrichum substriatum* in Central America that is more difficult to distinguish from other regional species of *Porotrichum* than the typical form of the species. In this form of *P. substriatum* (see, *e.g.*, *Allen 8741*, MO, NY), the plants are small with very short stipes. The stipe leaves in this form are poorly developed and are only wide-spreading rather than squarrose-recurved. The secondary stem and branch leaves are widely spaced, strongly complanate, and broadly ovate to oblong-ovate, with prorate leaf cells and costae that rarely end in a projecting spine.

The African distribution of *Porotrichum substriatum* given above reflects the synonymy of *Porotrichum caudatum* Broth. with *P. substriatum* (see Buck 1998).

10. *Porotrichum tenuinerve* B. H. Allen, Novon 4: 315. 1994. Protologue. Honduras. Lempira: Montaña de Celaque, trail from Camp Don Tomas to first ridge, 14°34′N, 88°39′W, *Allen 11338*. Types. Honduras. Lempira: Montaña de Celaque, trail from Camp Don Tomas to first ridge, 14°34′N, 88°39′W, *Allen 11338* (MO, holotype; NY, TEFH, isotypes).

Plants medium-sized, 3–6 cm high, stipitate-frondose, forming yellow green to green, lax tufts. Stolons creeping, evenly foliate; rhizoids smooth to lightly roughened, reddish brown, not or sparsely branched, in circular clusters just below the leaf insertions, on stolons, and at the base of stipitate stems; leaves loosely imbricate, widely spaced, triangular. Stems erect, stipitate, irregularly pinnate, complanate-foliate, at times flagellate-attenuate; stems in cross section with sclerodermis of 2–3 rows of small, thick-walled cells, grading into larger, firm-walled cortical cells, central strand well developed; paraphyllia absent; pseudoparaphyllia foliose. Stipes evenly foliate; leaves erect-spreading to spreading, ovate-triangular to triangular, acute to acuminate; margins entire to subserrulate. Stem leaves 2–3 mm long, flattened, oblong-cultriform, asymmetric, broadly acute, broadly apiculate; margins serrate or dentate at apex, teeth sometimes of 2–3 cells, serrulate to midleaf; costae very short and double or single and reaching 1/3 the leaf length; cells smooth, upper cells long-rhomboidal, 30–60 × 7–10 µm, median and basal cells linear-fusiform to vermicular, 50–90 × 6–10 µm; alar cells shorter, often porose, cells across the insertions yellow. Branch leaves similar to stem leaves except smaller and sometimes oval or spathulate. Gonioautoicous. Setae 15–20 mm long, reddish yellow. Capsules erect to suberect, ovoid-cylindrical, somewhat constricted at base, 1.5–2.0 mm long; exothecial cells small and thick-walled at mouth, rounded-rectangular, firm-walled below; stomata at base of capsules; opercula conic-rostrate, 1.5 mm long; annuli rudimentary; peristome diplolepideous; exostome teeth linear, 0.6–0.8 mm long, dorsal surface cross-striate and papillose below, vermiculate-papillose at middle, lightly papillose above, trabeculae and median line thin below, thickened above,

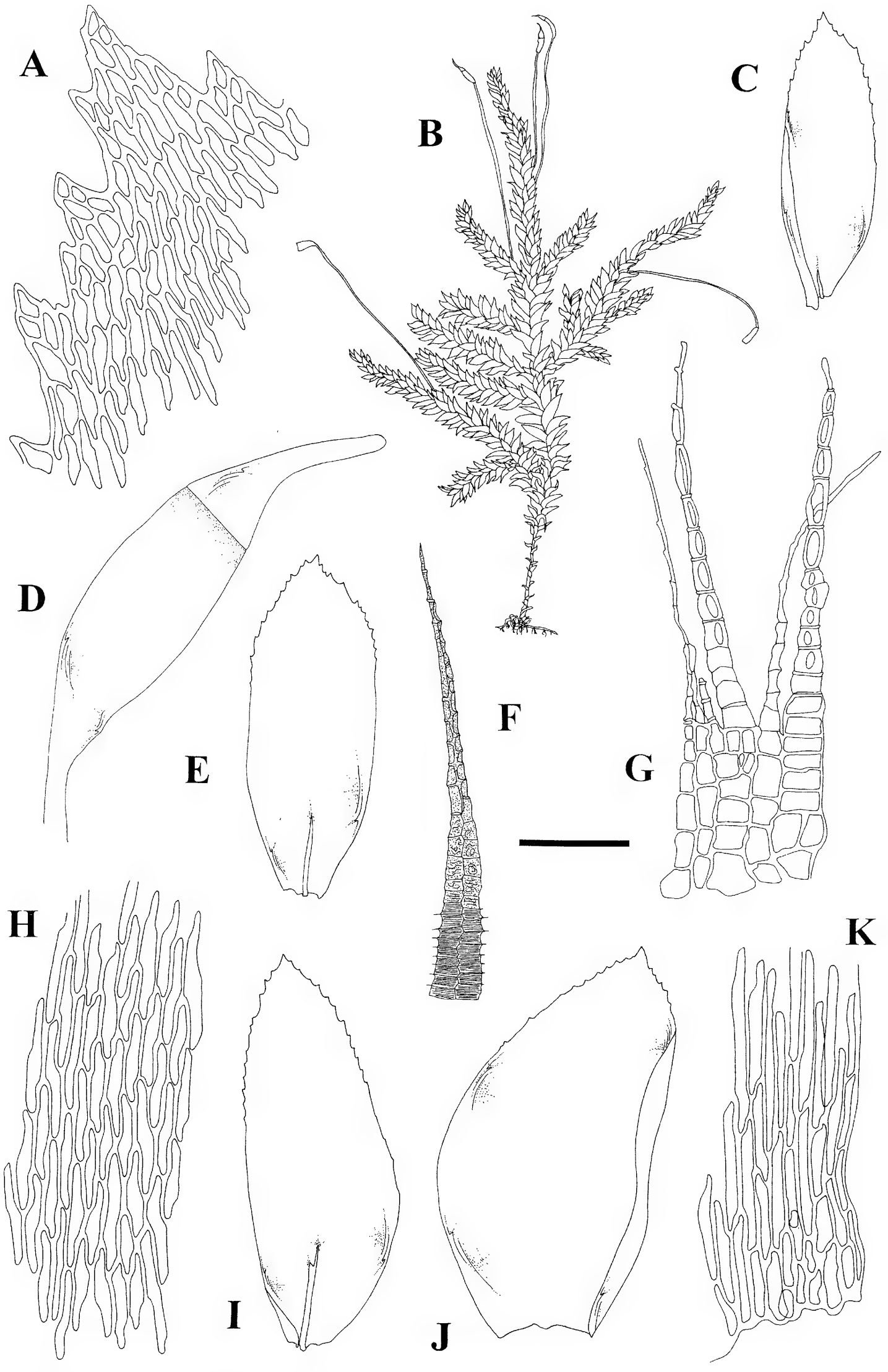
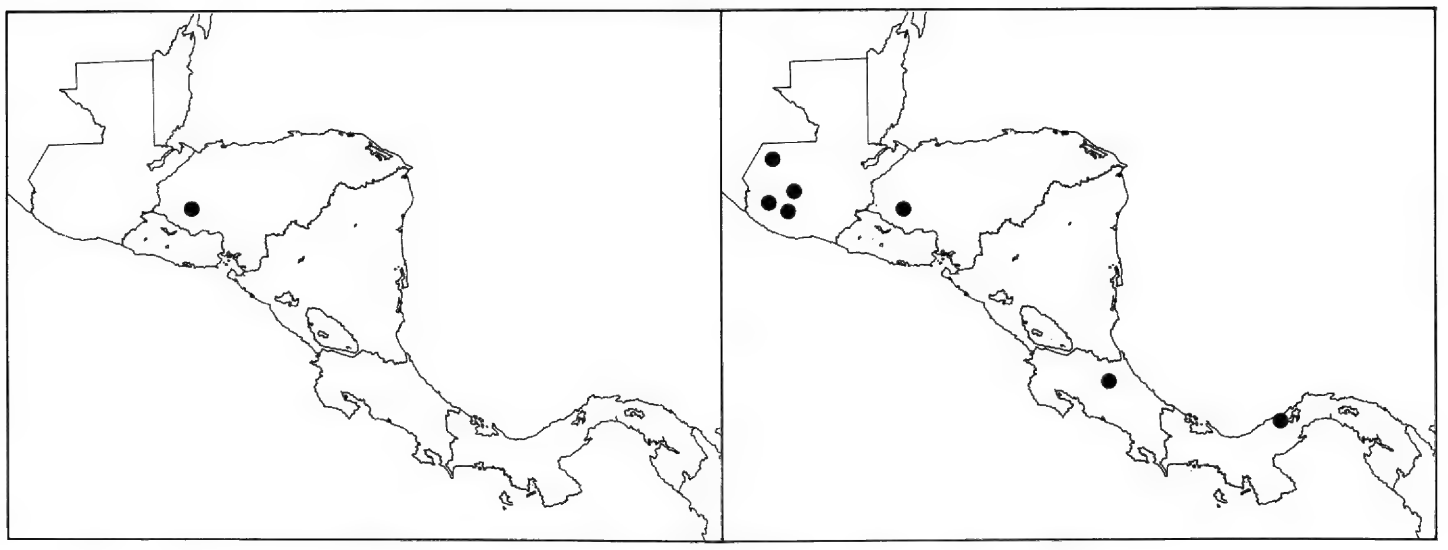


Figure 115. *Porotrichum tenuinerve*. A. Leaf apex. B. Habit. C & E. Branch leaves. D. Seta, capsule, and operculum. F. Exostome, dorsal (outer) surface. G. Endostome, ventral (inner) surface. H. Median leaf cells. I & J. Stem leaves. K. Basal and alar cells. Scale in mm: bar = 0.06 (A, H, K); bar = 0.13 (F, G); bar = 0.6 (C, E, I, J); bar = 0.8 (D); bar = 10.0 (B). All figure parts from *Allen 11334* (type).



Porotrichum tenuinerve *Porotrichum usagarum*

ventral surface with projecting trabeculae, lightly papillose; endostome lightly papillose, basal membranes 0.2 mm high, segments 0.4–0.5 mm long, broadly perforate, cilia 1–3, nodose, 0.30–0.35 mm long. Spores spherical, lightly papillose, 14–20 µm. Calyptrae tubular-cucullate, 2–3 mm long.

Illustrations. Allen (1994, Figs. 1–10). Figure 115.
Habitat. On twigs and roots; 2170–2180 m.
Distribution in Central America. HONDURAS. Lempira: *Allen 11334* (MO, TEFH).
World range: Central America.

Porotrichum tenuinerve is similar to *P. longirostre* in size and aspect, and to *P. mutabile* in its tendency to have multicellular, dentate teeth on the upper leaf margins. It differs from all Central American members of *Porotrichum* in having short costae (not more than 1/3 the leaf length) that may be double or single and a gonioautoicous sexual condition. Species of *Porotrichum* typically have slender costae that reach from 1/2–3/4 (rarely percurrent) the leaf length. While the short costa in *P. tenuinerve* seems exceptional, it actually represents the end of a morphological continuum within the genus. The gonioautoicous condition of *P. tenuinerve* is especially at odds with the other, consistently dioicous, Neotropical members of *Porotrichum*. Fleischer (1908) attributes the autoicous condition to the genus *Porothamnium*, which is here considered synonymous with *Porotrichum*.

11. *Porotrichum usagarum* Mitt., J. Linn. Soc., Bot. 22: 315. 1886. *Pinnatella usagara* (Mitt.) Broth., Nat. Pflanzenfam. I(3): 857. 1906. Protologue. Central Africa [Tanzania]. Usagara Mountains [*James Hannington*]. Type. Central Africa, Usagara Mts., 1882, *Rev. J. Hannington* (NY, holotype).

Porotrichum molliculum Broth., Bot. Jahrb. Syst. 24: 257. 1897. *Thamnium molliculum* (Broth.) Kindb., Hedwigia 41: 220. 1902. *Porothamnium molliculum* (Broth.) M. Fleisch. *ex* Broth., Nat. Pflanzenfam. (ed. 2) 11: 199. 1925. Protologue. Kilimandscharo: Landschaft Schira im Gürtelwalde an Bäumen beim Abstieg vom Kibo zur Culturregion 2500 m (*Volkens n. 1941*). Seengebiet: Ru-Nssóro, Wimi valley, an Bäumen c. 2100 m (*Scott Elliot n. 260*).

Porotrichum natalense Müll. Hal., Hedwigia 38: 129. 1899. *Porothamnium natalense* (Müll. Hal.) M. Fleisch., Musci Buitenzorg 3: 926. 1908. *Thamnium natalense* (Müll. Hal.) Kindb., Hedwigia 41: 239. 1902. Protologue. [South Africa] Prom. bonae spei, Natal, Inanda: *Dr. A. Rehmann* in Mus. A. A. *No. 334*, sub *Porotricho pennaeformi* var. *brachyphyllo* Rehm.

Porotrichum leavenworthii E. B. Bartram *in* Leavenw., Amer. Midl. Naturalist 36: 157. 1946 [July]. Protologue. Mexico: on tree trunks in moist shady places of cloud forest, Cerro Tancítaro, State of Michoacán, alt. 9,000 ft., July 25, 1940, *William Leavenworth, no. 18*. Type. Mexico, on tree in moist shade, cloud forest, Cerro Tancitaro, Michoacán, 9,000 ft., July 25, 1940, *William Leavenworth, No. 18* (MO, isotype), *syn. nov.*

Porotrichum guatemalense E. B. Bartram, Bryologist 49: 117. 1946 [December]. Protologue. Guatemala. Dept. Quetzaltenango: mountains southeast of Palestina on old road to San Juan Ostuncalco, *Standley*

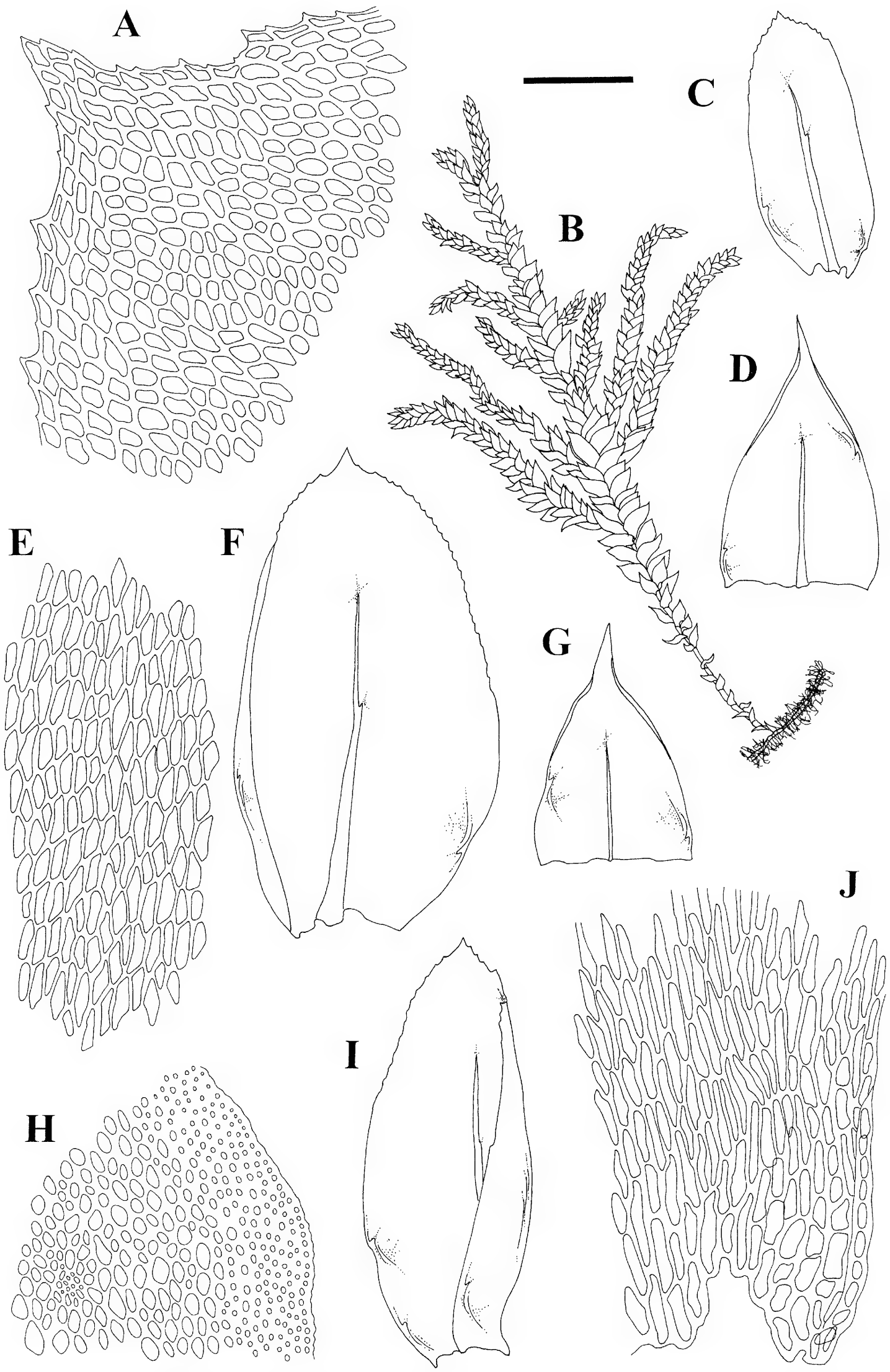


Figure 116. *Porotrichum usagarum*. A. Leaf apex. B. Habit. C. Branch leaf. D & G. Stipe leaves. E. Median leaf cells. F & I. Stem leaves. H. Stem in cross section. J. Basal and alar cells. Scale in mm: bar = 0.06 (A, E, J); bar = 0.08 (H); bar = 0.5 (C, D, F, G, I); bar = 6.4 (B). All figure parts from *Allen 12170*.

84288a. Types. Guatemala. Dept. Quetzaltenango: mountains southeast of Palestina on old road to San Juan Ostuncalco, *Standley 84288a* (FH, holotype; F, MO, isotypes), *syn. nov.*

Plants medium-sized to robust, to 6 cm high, stipitate-frondose, forming dull green to yellowish green, lax tufts. Stolons creeping, evenly foliate; rhizoids smooth to lightly roughened, reddish brown, not or sparsely branched, in circular clusters just below the leaf insertions, on stolons, and at the base of stipitate stems; leaves loosely imbricate, widely spaced, triangular. Stems erect, stipitate, irregularly pinnately branched, complanate-foliate, at times somewhat flagellate-attenuate; stems in cross section with sclerodermis of 5–8 rows of small, thick-walled cells, grading into larger, firm- to thick-walled cortical cells, central strand well developed; paraphyllia absent; pseudoparaphyllia foliose. Stipes evenly foliate; leaves widely spaced, spreading to squarrose, triangular to triangular-lanceolate, 1.0–1.2 mm long, acuminate; margins entire to subserrulate, narrowly recurved above; costae single and strong, ending 1/2–2/3 the leaf length. Stem leaves 0.5–2.0 mm long, erect-spreading, more or less flattened, concave, oblong-ovate, more or less symmetric, broadly acute, shortly decurrent; margins coarsely and irregular serrate above, more or less broadly inflexed below on one side; costae tapering at the ends, 2/3 the leaf length, often ending in a spine, sometimes spurred below, smooth on the dorsal surface; cells smooth, upper cells rounded-hexagonal, rhombic, subquadrate, 14–20 × 6–10 µm long, median cells rhomboidal, rhomboidal-fusiform to fusiform-elongate, (10–)20–40 × 4–8 µm; basal cells elongate-linear, cells at the extreme base porose; alar cells weakly differentiated as a few oblate, quadrate, or short-rectangular cells at the basal angles, cells across the insertions yellow. Branch leaves similar to stem leaves except smaller and sometimes ovate-spathulate. Asexual reproduction at times by axillary, flagellate branchlets. Dioicous. Setae 7– 10 mm long, reddish to yellow brown, smooth. Capsules erect to suberect, oblong to ovoid-cylindrical, 1.5 mm long; exothecial cells small and thick-walled at mouth, rounded-rectangular, firm-walled below; stomata at base of capsules; opercula conical, long-rostrate, 1.5–2.3 mm long; annuli rudimentary; peristome diplolepideous; exostome teeth linear, dorsal surface cross-striate and papillose below, papillose above, trabeculae and median line thin, ventral surface with projecting trabeculae, lightly papillose; endostome lightly papillose, basal membranes high, segments as long as exostome teeth, perforate, cilia rudimentary or absent. Spores spherical, lightly papillose, 12–15 µm. Calyptrae cucullate, smooth, lightly hairy.

Illustrations. Bartram (1949, Fig. 128 G–I); De Sloover (1983, Figs. 139–192); Enroth (1991b, Fig. 1); Sharp *et al.* (1994, Fig. 568); Magill and Rooy (1998, Fig. 166 10–14); Buck (2003, Fig. 110). Figure 116.

Habitat. On trees and rocks of dry cliff faces; 1900–2850 m.

Distribution in Central America. GUATEMALA. Chimaltenango: *Godman & Salvin* (MO); Huehuetenango: *Laeger 3686* (MO); Quetzaltenango: *Standley 84288a* (F, FH); Sololá: *Steyermark 47568* (F, FH, MO). HONDURAS. Lempira: *Allen 12170* (MO). COSTA RICA. Heredia: *Crosby 9903* (MO). PANAMA. Colón: *Crosby 10353* (MO).

World range: Mexico; Central America; Northern South America; West-Central, East, and South Tropical Africa, Southern Africa, Western Indian Ocean.

Porotrichum usagarum is a medium-sized to robust species with spreading to squarrose stipe leaves. The outstanding characteristic of the species is found in its upper leaf cells, which are short and often rhombic. It is the only Central American species of *Porotrichum* with this distinctive feature. The species is more likely to be confused with *Homaliodendron piniforme*, *Pinnatella minuta*, or *Thamnobryum tumidicaule*, all of which have short, isodiametric to rhombic upper leaf cells. *Homaliodendron piniforme* and *Pinnatella minuta* are considerably smaller plants than *Porotrichum usagarum*, and both species have less strongly serrate upper leaf margins as well as short rather than elongate median leaf cells. Furthermore, *Homaliodendron piniforme* differs from *Porotrichum usagarum* in lacking a stem central strand, while *Pinnatella minuta* has an intramarginal limbidium in the basal region of its leaves. *Thamnobryum tumidicaule* is similar in size to *Porotrichum usagarum* and both species have elongate basal leaf cells. It differs from *Porotrichum usagarum* in having strong, evenly thickened costae.

Porotrichum usagarum has long been known in Central America as *P. guatemalense*. The type of *P. usagarum* differs from *P. guatemalense* in having ovate to broadly ovate, often asymmetric stem leaves with stronger costae that consistently end in spines and are often toothed on the dorsal surface. Enroth and Hodgetts (1996), however, found that *P. usagarum* represents one end of an extremely variable species complex. At the other end of the complex is the African *P. molliculum* Broth., which appears identical to the Central American *P. guatemalense* in leaf and costa form. Since the complex exhibited continuous variation Enroth and Hodgetts (1996) concluded it represented ecotypes of a single species. In this respect it is interesting to note that Mexican collections named *P. guatemalense* approach closely the type form of *P. usagarum*, while plants from Suriname (*Allen 25555*, MO) are identical to it.

Porotrichum leavenworthii differs from *P. usagarum* in having remarkably short (sometimes only 10 µm long) median leaf cells, but otherwise falls within the variation of *P. usagarum*. The name *P. leavenworthii* (July 1946) predates *P. guatemalense* (December 1946), which is in general use for this species in Guatemala (Bartram 1949) and Mexico (Smith 1994).

10. *Thamnobryum* Nieuwl., Amer. Midl. Naturalist 5: 50. 1917, new name for *Thamnium* Schimp. *in* B.S.G., Bryol. Eur. 5: 211. 1852 (fasc. 49–51), illegitimate homonym, not *Thamnium* Vent., 1799, nor *Thamnium* Klotzsch, 1838. *Hypnum* Hedw. sect. *Thamnium* (Schimp.) Sull. *in* A. Gray, Manual (ed. 2), 669. 1856. *Neckera* Hedw. sect. *Thamnium* (Schimp.) Mitt., J. Linn. Soc., Bot. 4: 89. 1859. *Porotrichum* (Brid.) Hampe sect. *Thamnium* (Schimp.) Mitt., J. Linn. Soc., Bot. 12: 459. 1869. *Hypnum* Hedw. subgen. *Thamnium* (Schimp.) Hobk., Syn. Brit. Mosses 145. 1873.

Arbuscula H. A. Crum & L. E. Anderson, Bryologist 67: 163. 1964, superfluous name, new name for *Thamnium* Schimp. *in* B.S.G., Bryol. Eur. 5: 211. 1852 (fasc. 49–51).

Plants medium-sized or robust, stipitate-frondose, forming dark green to yellowish green, lax tufts. Stolons creeping, evenly foliate; rhizoids smooth, reddish brown, not or sparsely branched, restricted to stolons and the bases of stipitate stems; leaves scale-like, widely spaced, broadly triangular. Stems erect, stipitate, irregularly pinnately branched, variously complanate-foliate, at times with flagellate-attenuate tips; in cross section with sclerodermis of small, thick-walled cells, grading into larger, thick-walled cortical cells, central strand poorly developed; paraphyllia absent; pseudoparaphyllia foliose. Stipes evenly foliate; leaves appressed with or without erect-spreading or squarrose tips, decurrent, ovate-triangular to triangular, acute to acuminate; margins entire to subserrulate; costae single and strong, ending near apex. Stem leaves erect-spreading, arched-incurved or flattened when dry, smooth or plicate, ovate-lanceolate, ovate, oblong-ovate, or ovate-ligulate, more or less symmetric, obtuse, broadly rounded, broadly acute to short-acuminate, sometimes apiculate or mucronate, shortly decurrent; margins serrate above, teeth unicellular or multicellular, serrulate below, usually shortly incurved below on one side, or plane throughout; costae single, strong, ending near the apex, often sinuose and forked or spurred; cells smooth or prorate, at times porose, upper cells between the end of the costa and the apex isodiametric, irregularly rounded, rhomboidal or shortly fusiform, apical cells oblate, isodiametric, hexagonal, rhomboidal, or subrectangular, often irregular and rounded, median cells rhomboidal-fusiform to fusiform-elongate; basal cells elongate-linear, porose; alar cells not or weakly differentiated. Branch leaves similar to stem leaves, except smaller. Asexual reproduction by axillary, microphyllous, flagelliform branches. Dioicous. Setae elongate, smooth, red brown. Capsules horizontal to pendent, cylindrical; exothecial cells short-rectangular; stomata present; opercula obliquely conic-rostrate, annuli rudimentary, of 2 rows of thick-walled cells; peristome diplolepideous; exostome teeth narrowly triangular, dorsal surface cross-striate in lower 3/4, ventral trabeculae strongly developed; endostome as long as exostome teeth, basal membranes high, segments well developed, papillose, keeled, perforate, cilia usually well developed. Calyptrae cucullate, naked.

Thamnobryum is a handsome genus of frondose or stipitate mosses with 42 species (Crosby *et al.* 2000) distributed throughout the world. The genus is usually included in the subfamily Thamnioideae of the Neckeraceae (Fleischer 1905b, 1906; Brotherus 1906c, 1925; Robinson 1975; Crum & Anderson 1981; Vitt 1984; Enroth 1989, 1994b; Buck 1998; Buck & Goffinet 2000; Goffinet & Buck 2004).

Mönkemeyer (1927), however, placed the genus (as *Thamnium*, an illegitimate name) in its own family. This family (now the Thamnobryaceae) has been expanded by Margadant and During (1982), Walther (1983), Buck and Vitt (1986), Sastre (1987), and Churchill and Linares (1995) to include all members of the Neckeraceae with a frondose or stipitate habit and striate exostomes. Buck (1998), however, pointed out that some thamnioid genera are weakly stipitate, and both striate and papillose exostomes can be found in the thamnioid as well as the neckeroid genera. The taxonomy of the Thamnioideae is so unsettled that Robinson (1975) characterized them as a ". . . vile group of genera. . . . " This is because most important gametophytic character states within the group are not discrete, and while many of its critical characters are sporophytic, the group is mainly dioicous and collections often lack sporophytes.

In addition to its usually large size and strongly stipitate-frondose growth form, *Thamnobryum* is characterized by stems that have a weak central strand and lack paraphyllia. Its more or less symmetric leaves have strong, single costae that do not taper above and end at or near the apex. The often spurred or forked costae are somewhat sinuose. Although none of the Central American species of *Thamnobryum* has costae with abaxial teeth or terminal spines, Enroth (1994b) considered such structures characteristic of the genus. The apical leaf cells in *Thamnobryum* are typically short, and the alar cells are either not or very weakly differentiated. Sporophytically, *Thamnobryum* has very long, smooth setae, inclined to pendent, asymmetric capsules, and a well-formed hypnoid peristome. Enroth (1994a, b) considered *Thamnobryum* to be the most primitive genus in the Neckeraceae on the basis of both its gametophyte and sporophyte features.

In the Neotropics *Thamnobryum* is most easily confused with *Porotrichum*. It differs from that genus in having the combination of duller plants with stronger costae and shorter apical leaf cells. *Homaliodendron* is similar in size to *Thamnobryum*, but it differs in lacking a stem central strand and in having more asymmetric leaves with weaker costae. The leaves of *Pinnatella* are similar to those of *Thamnobryum* in having strong, single costae and short upper leaf cells. In the Neotropics, however, its plants are usually considerably smaller than those of *Thamnobryum*, and its leaves have short, usually isodiametric median cells as well as a basal intramarginal border of elongate cells. *Porotrichodendron* can also be similar in size to *Thamnobryum*. It differs, however, in having leaves that are rounded or auriculate at the insertions.

The name *Thamnobryum* combines the Greek *thamnos* (bush or shrub) with the generic name *Bryum* and refers to the stipitate-frondose growth form of the genus.

Key to the Neotropical species of *Thamnobryum*

1. Secondary stem and branch leaves ligulate to lingulate; costae to 160 µm wide at base. . . . . [2. *T. liesneri*]
1. Secondary stem and branch leaves oblong-ligulate, oblong-ovate, ovate to ovate-lanceolate; costae 40–60 µm wide at base 2

2. Plants robust, 5–13 cm high; upper stipe leaves 2.0–2.5 mm long; stem leaves complanate and distinctly plicate when dry, oblong-ligulate, rounded-apiculate, apical cells above the costa hexagonal, marginal teeth 1-celled . . . . . 1. *T. fasciculatum*
2. Plants medium-sized, 2–4(–8) cm high; upper stipe leaves 0.8–1.0 mm long; stem leaves arched-incurved and lightly plicate to smooth when dry, ovate to ovate-lanceolate, acute, apical cells above the costa mostly fusiform to rhomboidal, marginal teeth 1–3-celled . . . . . 3. *T. tumidicaule*

1. *Thamnobryum fasciculatum* (Sw. *ex* Hedw.) I. Sastre *in* I. Sastre & W. R. Buck, Caribbean J. Sci. 29: 32. 1993. *Hypnum fasiculatum* Sw. *ex* Hedw., Sp. Musc. Frond. 245. 1801. *Neckera fasciculata* (Sw. *ex* Hedw.) Arn., Mém. Soc. Linn. Paris 5: 292. 1826. *Porotrichum fasciculatum* (Sw. *ex* Hedw.) Mitt., J. Linn. Soc., Bot. 12: 468. 1869. *Thamnium fasciculatum* (Sw. *ex* Hedw.) Müll. Hal., Hedwigia 37: 260. 1898. *Porothamnium fasciculatum* (Sw. *ex* Hedw.) M. Fleisch., Musci Buitenzorg 3: 927. 1908. Protologue. Locus Jamaica [*Swartz*].

Plants robust, 5–13 cm high, stipitate-frondose, forming dark green to yellowish green, lax tufts. Stolons creeping, evenly foliate; rhizoids smooth, reddish brown, not or sparsely branched, in circular clusters just below the leaf insertions, on stolons, and at the base of stipitate stems; leaves loosely

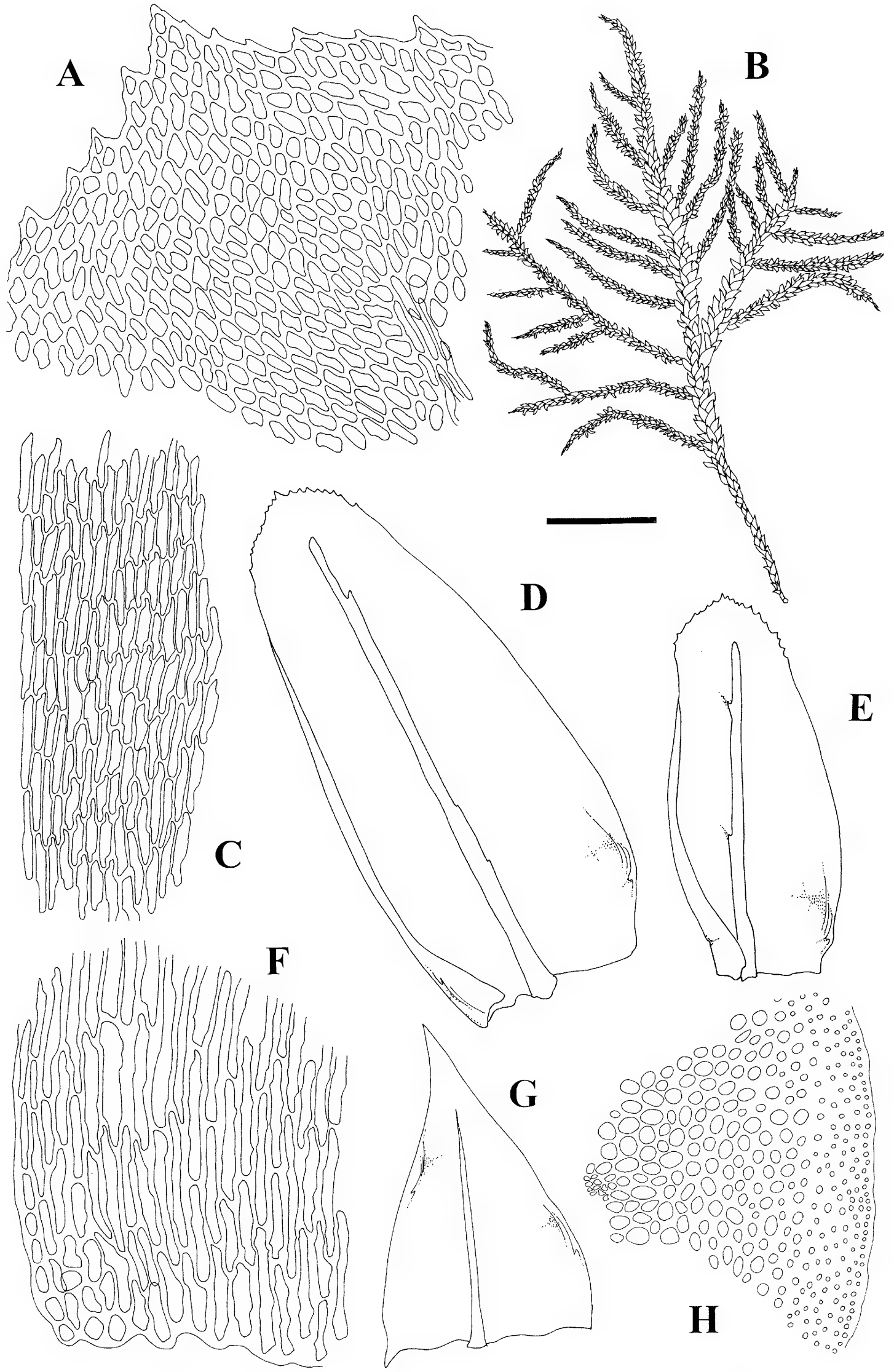
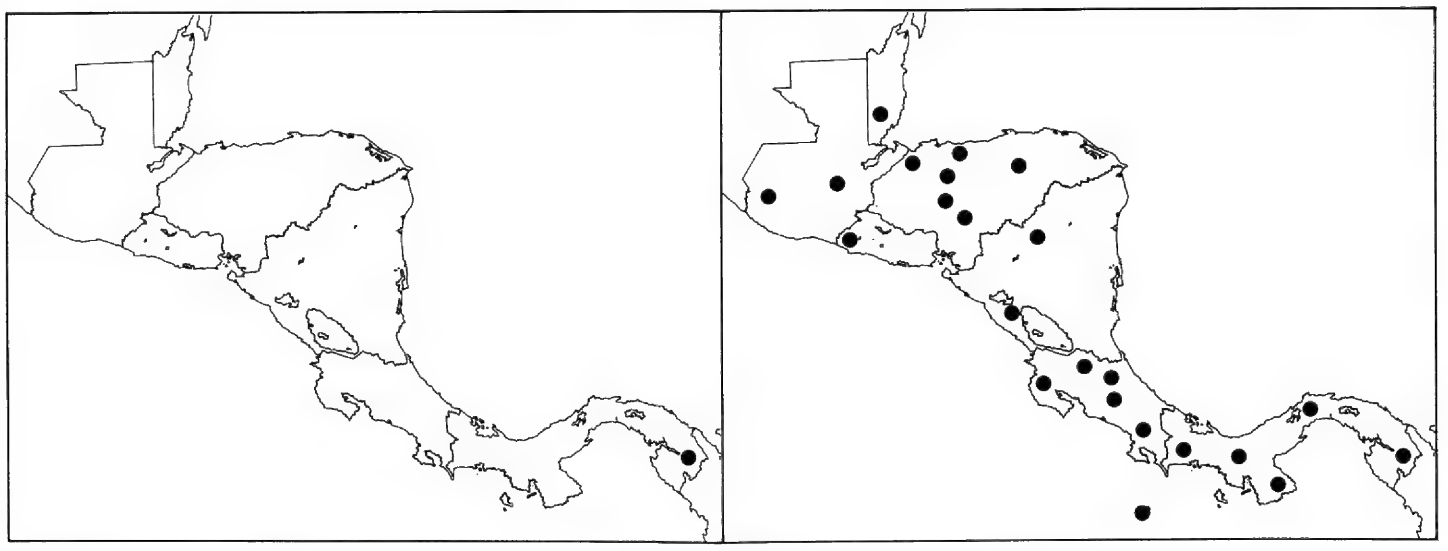


Figure 117. *Thamnobryum fasciculatum*. A. Leaf apex. B. Habit. C. Median leaf cells. D. Stem leaf. E. Branch leaf. F. Basal and alar cells. G. Stipe leaf. H. Stem in cross section. Scale in mm: bar = 0.06 (A, C, F); bar = 0.08 (H); bar = 0.5 (D, E); bar = 0.6 (G); bar = 12.7 (B). All figure parts from *Mori & Gentry 4496*.



Thamnobryum fasciculatum *Thamnobryum tumidicaule*

imbricate, widely spaced, broadly triangular. Stems erect, stipitate, irregularly pinnate, complanate-foliate, at times flagellate-attenuate; stems in cross section with sclerodermis of 5–7 rows of small, thick-walled cells, grading into somewhat larger, thick-walled cortical cells, central strand poorly developed; paraphyllia absent; pseudoparaphyllia foliose. Stipes evenly foliate; leaves appressed below, erect-spreading above, 2.0–2.5 mm long, ovate-triangular to triangular, acute to acuminate, decurrent; margins entire to subserrulate; costae single and strong, ending 1/2–2/3 the leaf length. Stem leaves erect-spreading, flattened, plicate, 3–4 mm long, ovate-ligulate, more or less symmetric, broadly rounded to obtuse, sometimes apiculate or mucronate, shortly decurrent; margins serrate above, teeth unicellular, serrulate below, usually shortly incurved below on one side, or plane throughout; costae single, strong, ending near the apex, often sinuose and forked or spurred; cells smooth or prorate, upper cells isodiametric, irregularly rounded, rounded-hexagonal, subrhomboidal, subquadrate, or oblate, 8–20 × 4–10 µm, median cells rhomboidal-fusiform to fusiform-elongate, 26–50 × 4–6 µm, median marginal cells linear, in 2–3 rows; basal cells elongate-linear, 40–90 × 6 µm, porose; alar cells not or weakly differentiated as oblate, quadrate, or short-rectangular cells at the basal angles. Branch leaves similar to stem leaves except smaller and marginal teeth at apex better developed. Dioicous. Sporophytes unknown in Central America, description from Buck (1998) and Sastre (1987). Setae elongate, 1.5–2.5 cm long, smooth, red brown. Capsules horizontal to pendent, cylindrical, 1.6–2.8 mm long; exothecial cells short-rectangular, firm- to thick-walled, not smaller at the mouth; stomata present; opercula obliquely conic-rostrate, 1.4 mm long; annuli rudimentary, of 2 rows of thick-walled cells; peristome diplolepideous; exostome teeth narrowly triangular, dorsal surface cross-striate in lower 3/4, papillose above, ventral trabeculae strongly developed; endostome as long as exostome teeth, basal membranes high, smooth to sparsely papillose, segments well developed, papillose, keeled, perforate, cilia in groups of three, appendiculate. Spores 10–14 µm, more or less smooth. Calyptra not seen.

Illustrations. Hedwig (1801, Pl. 62 8–10); Churchill and Linares (1995, Fig. 191 h–n); Buck (1998, Pl. 46 1–11); Gradstein *et al.* (2001, Fig. 217 N–T). The illustration of *T. fasciculatum* in Duarte Bello (1997, Pl. 216) appears to be *T. tumidicaule*. Figure 117.

Habitat. On soil along streams and on ground; 1200–1768 m.

Distribution in Central America. PANAMA. Darién: *Mori & Gentry 4310* (MO).

World range: Central America; Caribbean; Western, Northern, and Southern South America, Brazil.

Thamnobryum fasciculatum is a robust species with well-developed stipitate stems and complanate, distinctly plicate stem leaves. Its ovate-ligulate leaves are broadly rounded at the apex and have strong, single costae that are more or less equal in width throughout the leaf. The costae end near the apex; they are somewhat sinuose and often forked or spurred below. The upper leaf margins of the secondary stem and branch leaves are sharply serrate, but the teeth on the stem leaves are unicellular

while those on the branch are both uni- and multicellular. Although the median and basal leaf cells in *T. fasciculatum* are elongate, the apical cells, especially those between the end of the costa and the leaf apex, are short and mostly oblate to hexagonal or rhombic.

The only other *Thamnobryum* species in Central America, *T. tumidicaule*, is considerably smaller than *T. fasciculatum*, with most plants only 2–4 cm high. Its stem leaves are arched and incurved rather than complanate when dry, and at best they are only weakly plicate. In addition, the stem leaves of *T. tumidicaule* are ovate to ovate-lanceolate and distinctly acute rather than rounded to obtuse. Microscopically, the upper leaf cells of the stem leaves between the end of the costa and the apex are longer (fusiform to rhomboidal) than in *T. tumidicaule*, and the marginal teeth at the apex are often multicellular.

Most Central American species of *Porotrichum* differ from *T. fasciculatum* in having shorter, weaker costae that taper at the ends, and in having elongate upper leaf cells. *Porotrichum evansii* is an odd *Porotrichum* marked by upper leaves that have percurrent costae, which often fill the apices. It differs from *T. fasciculatum* in its smaller size and in having elongate upper leaf cells. *Homaliodendron flabellatum* is similar in size to *Thamnobryum fasciculatum*. It differs, however, in having asymmetric, oblong-ovate leaves with large, multicellular marginal teeth, and stems that lack a central strand.

2. *Thamnobryum liesneri* B. H. Allen & S. P. Churchill, Novon 12: 155. 2002. Protologue. Venezuela. Amazonas: Atures, lower forested E slope of unnamed 1760 m peak, 8 km NW of settlement of Yutaje, 3 km W of Río Coro-Coro, W of Serranía de Yutaje, *Liesner & Holst 21891* Types. Venezuela. Amazonas: Atures, lower forested E slope of unnamed 1760 m peak, 8 km NW of settlement of Yutaje, 3 km W of Río Coro-Coro, W of Serranía de Yutaje, *Liesner & Holst 21891* (MO, holotype; H, NY, US, VEN, isotypes).

Plants slender, dull, light green, older plants black brown, in dense wiry tufts to 4 cm high. Stolons creeping; rhizoids in circular clusters on the parts that touch the substrate, red, smooth; leaves widely spaced, reduced, hastate, to 0.5 mm long; costae single, strong. Stems erect, stipitate below, weakly frondose above, irregularly 1–2-pinnately branched; stems in cross section with 6–8 rows of small, thick-walled epidermal cells, cortical cells firm-walled, hyaline, central strand weakly developed; paraphyllia absent; pseudoparaphyllia foliose; rhizoids densely clustered at base of stems; stems and branches often ending in flagellate tips. Stipe leaves erect to erect-spreading when dry, erect-spreading when wet, widely spaced, hastate near base, linear-lanceolate above, 1.0–1.8 mm long. Stem and branch leaves erect to erect-incurved when dry, well spaced, ligulate to lingulate, 1.7–2.0 mm long, flat to variously concave, apices acute; margins entire in lower 1/2–3/4, irregularly toothed to crenulate at apex, plane to reflexed below; lamina unistratose above, uni- or bistratose at base; costae single, very broad (to 160 µm wide at base), subpercurrent, often forked at apex, usually spurred below; leaf cells firm-walled, smooth, not porose, apical cells irregularly rhomboid to hexagonal, 12–20 × 6–10 µm, upper median cells fusiform-rhomboid, usually obliquely arranged from costa; basal cells oblong-rectangular, 20–40 × 6–8 µm; alar cells short, weakly differentiated. Dioicous (?). Sporophytes unknown.

Illustrations. Allen and Churchill (2002, Fig. 1). Figure 118.
Habitat. On boulders near stream; 1050–1200 m.
Not yet known from Central America.
World range: Northern South America.

Thamnobryum liesneri differs from all other species of *Thamnobryum* by its ligulate to lingulate stem and branch leaves that have very broad (to 160 µm and a third or more of the leaf base width), strongly forked and spurred subpercurrent costae. Although there are some species of *Thamnobryum* from the Juan Fernández Islands with costae to 100 µm wide, these species have ovate-lanceolate or lanceolate leaves with percurrent or excurrent costae. All species of *Porotrichum* differ from *T. liesneri* in having leaves with more slender costae and longer upper cells.

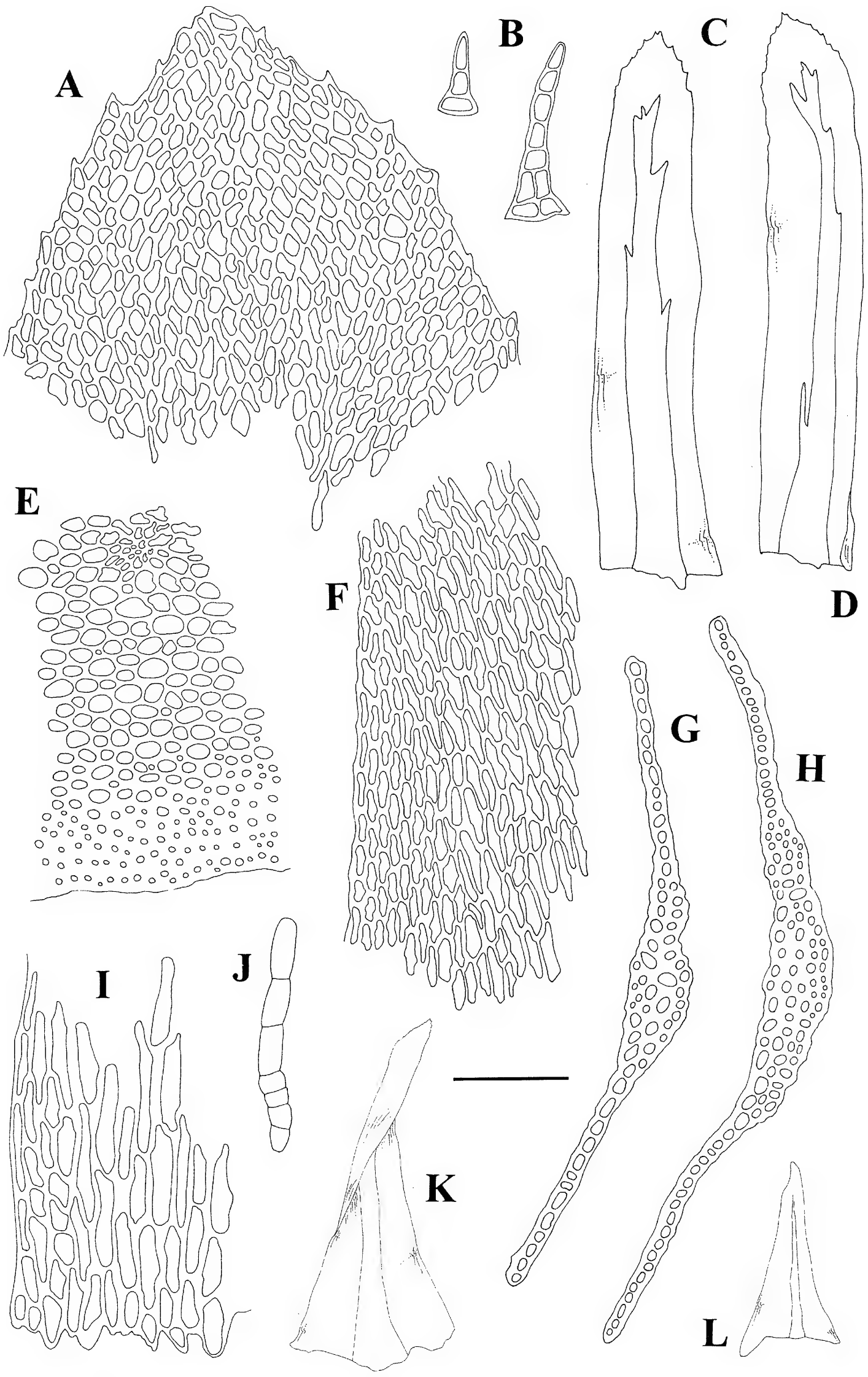


Figure 118. *Thamnobryum liesneri*. A. Leaf apex. B. Pseudoparaphyllia. C & D. Secondary stem leaves. E. Stem in cross section. F. Median leaf cells and margin. G. Cross section, upper part of stem leaf. H. Cross section, lower part of stem leaf. I. Basal and alar cells. J. Axillary hair. K. Stipe leaf. L. Primary stem leaf. Scale in mm: bar = 0.05 (B, J); bar = 0.06 (A, E–I); bar = 0.34 (K, L); bar = 0.4 (C, D). All figure parts from *Liesner & Holst 21891* (type).

3. *Thamnobryum tumidicaule* (K. A. Wagner) F. D. Bowers, Bryologist 77: 162. 1974. *Thamnium tumidicaule* K. A. Wagner, Bryologist 55: 145. 1952. Protologue. Costa Rica. Río Reventazón below Santiago, Prov. of Cartago, Costa Rica, *C. W. Dodge 8251*. Type. Plants of Costa Rica. Cartago Province. Flood plain of Río Reventazón below Santiago, 740–750 m, May 23, 1930, *C. W. Dodge No. 8251* (MO, isotype).

Plants medium-sized, 2–4(–8) cm high, stipitate-frondose, somewhat flattened, forming dark green, occasionally yellowish green, lax tufts. Stolons evenly foliate, creeping; rhizoids smooth, reddish brown, not or sparsely branched, in circular clusters just below the leaf insertions, on stolons, and at the base of stipitate stems; leaves appressed, widely spaced, broadly triangular. Stems erect, stipitate, irregularly pinnate, complanate-foliate, at times flagellate-attenuate; stems in cross section with sclerodermis of 4–7 rows of small, thick-walled cells, grading into somewhat larger, firm- to thick-walled cortical cells, central strand poorly developed; paraphyllia absent; pseudoparaphyllia foliose. Stipes evenly foliate; leaves erect-spreading, 0.9–1.0 mm long, ovate-triangular to triangular, broadly acuminate, decurrent; margins subserrulate above; costae single and strong, ending 1/2–2/3 the leaf length. Stem leaves arched-incurved and lightly plicate to smooth when dry, erect-spreading to spreading, somewhat flattened when wet, 2–3 mm long, ovate to ovate-lanceolate or oblong-ovate, more or less symmetric, broadly acute to short-acuminate, shortly decurrent; margins serrate above, teeth unicellular or multicellular, serrulate below, usually shortly incurved below on one side, or plane throughout; costae single, strong, ending near the apex, often sinuose and spurred; cells smooth, at times lightly porose, upper cells between the end of the costa and the apex rhomboidal to shortly fusiform, apical cells irregularly hexagonal, isodiametric, or subrectangular, 8–20 × 6–10 µm, median cells rhomboidal-fusiform to fusiform-elongate, 20–40 × 6–10 µm; basal cells elongate-linear, 30–70 × 4–6 µm; alar cells not or weakly differentiated as oblate, quadrate, or short-rectangular cells at the basal angles. Branch leaves similar to stem leaves except smaller, more flattened, often obovate. Asexual reproduction by axillary, microphyllous, flagelliform branches. Dioicous. Sporophytes unknown.

Illustrations. Wagner (1952, Figs. 1–6); Sharp *et al.* (1994, Fig. 570); Duarte Bello (1997, Pl. 216, as *Porotrichum fasciculatum*); Buck (1998, Pl. 46 12–20). Figure 119.

Habitat. On wet rocks, often in or on stream banks, boulders in forest, and limestone outcrops; 220–2450 m.

Distribution in Central America. BELIZE. Toledo: *Whittemore 5628* (MO). GUATEMALA. El Progreso: *Sharp 5082* (F); Quetzaltenango: *Standley 86645* (F, FH). EL SALVADOR. Ahuachapan: *Davidse et al. 37473* (BM, MO). HONDURAS. Atlántida: *Allen 17441* (MO, TEFH); Cortés: *Standley et al. 7046* (F); Comayagua: *Allen 13685* (MO); Francisco Morazán: *Allen 12381* (MO); Olancho: *Allen 12572* (MO); Yoro: *Allen 13637* (MO). NICARAGUA. Granada: *Granzow de la Cerda & Moreno GC-1503* (DUKE, MO); Jinotega: *Stevens & Grijalva 15355* (MO). COSTA RICA. Alajuela: *Lyon 600* (MO); Cartago: *Dodge 8251* (MO); Guanacaste: *Holz & Schäfer-Verwimp CR 00-0006* (MO); Heredia: *Crosby 9889* (CR, MO, US); Puntarenas: *Lyon 312* (CR, MO), Cocos Island: *Gómez 6571* (MO). PANAMA. Chiriquí: *Croat 48842* (MO, NY, PMA); Darién: *Allen 8751* (MO, NY); Los Santos: *Hammel 5440* (MO); Panamá: *Crosby 10102* (MO); Veraguas: *Crosby 10146* (MO).

World range: Mexico; Central America; Caribbean.

Thamnobryum tumidicaule is a medium-sized species (usually 2–4 cm high) with well-developed stipitate stems. Its stem leaves are arched-incurved and vary from smooth to lightly plicate when dry. The stem leaves can be ovate to ovate-lanceolate or oblong-ovate, are broadly acute to shortly acuminate, and have strong, single costae that are more or less equal in width throughout the leaf. The costae end near the apex; they are somewhat sinuose and often spurred below. The upper leaf margins of the secondary stem and branch leaves are sharply serrate, and the marginal teeth are often multicellular. Although the median and basal leaf cells in *T. tumidicaule* are mostly fusiform-elongate or elongate-linear, the upper leaf cells are short, irregularly hexagonal, isodiametric, or subrectangular, and the apical cells between the end of the costa and the leaf apex are rhomboidal to shortly fusiform.

The only other *Thamnobryum* species in Central America, *T. fasciculatum*, is presently known only from Panama. It is considerably larger than *T. tumidicaule*, with plants varying from 5 to 13 cm

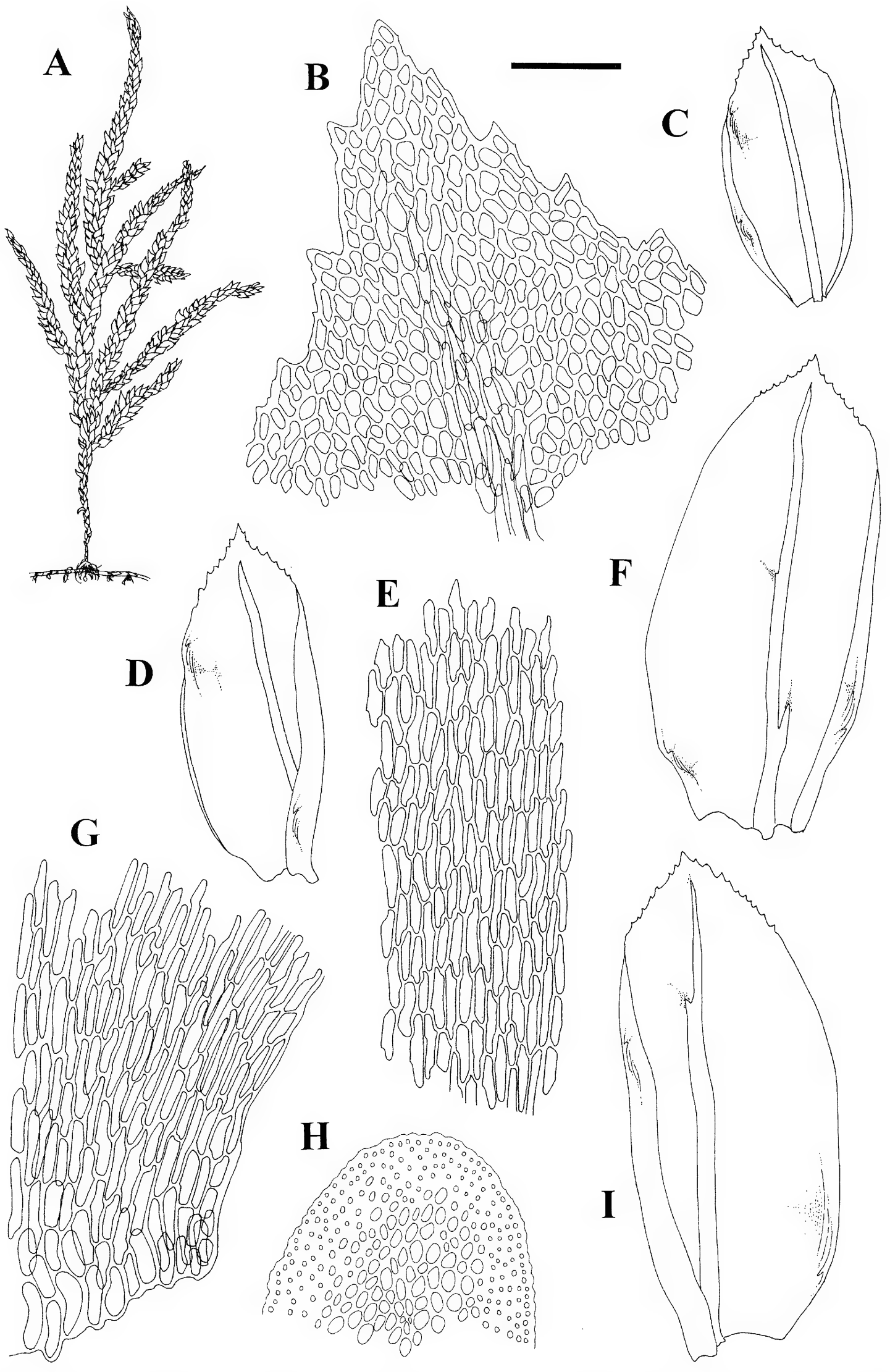


Figure 119. *Thamnobryum tumidicaule*. A. Habit. B. Leaf apex. C. Stipe leaf. D. Branch leaf. E. Median leaf cells. F & I. Stem leaves. G. Basal and alar cells. H. Stem in cross section. Scale in mm: bar = 0.06 (B, E, G); bar = 0.08 (H); bar = 0.5 (C, D, F, I); bar = 8.0 (A). A, H from *Allen 17582*; all other figure parts from *Dodge 8251* (type).

high. Its oblong-ligulate to ligulate stem leaves are strongly complanate, distinctly plicate when dry, and rounded- or obtuse-apiculate. Microscopically, the upper leaf cells of the stem leaves between the end of the costa and the apex in *T. fasciculatum* are shorter (hexagonal) than in *T. tumidicaule*, and the marginal teeth at the apex are unicellular.

Thamnobryum tumidicaule differs from most Central American species of *Porotrichum* in having strong, evenly thickened costae and short, apical leaf cells. *Porotrichum evansii* could be confused with *T. tumidicaule*, because it is more or less similar in size and often has upper leaves with percurrent costae that fill the apex. It differs from *T. fasciculatum* in having complanate stem leaves and elongate upper leaf cells. *Homaliodendron flabellatum* is similar in to *Thamnobryum tumidicaule* in having multicellular marginal teeth. It differs, however, in its more robust size (3–10 cm high) and in having asymmetric, oblong-ovate leaves and stems that lack a central strand.

PILOTRICHACEAE

Pilotrichaceae Kindb., Bot. Centralbl. 77: 54. 1899.

Callicostaceae H. A. Crum, Bryologist 87: 210. 1984.

Plants medium-sized to large, sometimes slender and wiry. Stolons creeping; rhizoids from clusters of initials abaxial to the leaf insertions, on stolons, and at the base of primary stems. Stems erect to pendent, typically stipitate, regularly pinnately to bipinnately branched; branches determinate or indeterminate, evenly foliate; stems in cross section with a well-developed sclerodermis (sometimes with a unistratose hyalodermis), central strand absent; paraphyllia absent; pseudoparaphyllia narrowly foliose to filamentous; axillary hairs 2-celled. Stipe leaves appressed or appressed below and squarrose above; margins often narrowly recurved. Stem and branch leaves smooth or undulate to rugose, decurrent; margins subentire, serrulate, or serrate, plane, recurved or inflexed, at times bordered by elongate to sigmoid cells; costae strong, double, reaching above midleaf, often subpercurrent, parallel or diverging throughout, at times with a dorsal crest, usually ending in a stout tooth, in cross section with homogeneous, thick-walled cells; cells short, thick-walled, smooth or prorate, occasionally porose; alar cells not or weakly differentiated. Asexual propagula often present on costae or leaf margins. Dioicous, synoicous, or autoicous. Setae short, flexuose, smooth or roughened above. Capsules exserted or immersed, erect, oblong-cylindric, symmetric; exothecial cells thick-walled; stomata usually present; opercula short-rostrate; annuli rudimentary; peristome diplolepideous; exostome teeth pale yellow, narrowly triangular, dorsal (outer) surface papillose throughout, trabeculae and median line faint; endostome yellow, lightly papillose throughout, basal membranes low, segments not or narrowly perforate, not keeled, cilia rudimentary or absent. Calyptrae mitrate, with archegonia and/or sparse hairs.

The Pilotrichaceae have had a complicated history, due in part to their closeness to the Hookeriaceae and Daltoniaceae, and in part to the classic moss dilemma: conflicting systematic evidence provided by their gametophytes on one hand and sporophytes on the other. The Pilotrichaceae were originally proposed as a monogeneric family (Kindberg 1899), and later expanded to include *Pilotrichidium* (Brotherus 1907c, 1925; Fleischer 1923). Miller (1971) placed 15 genera in the family on the basis of character state polarity established through the application of 23 principles for moss systematics. Crosby (1974b), in a classification based principally on peristome structure, synonymized the family with the Daltoniaceae. Buck (1987, 1988) emphasized gametophytic rather than sporophytic characters in re-establishing the Pilotrichaceae (as Callicostaceae) for 23 genera. A molecular and morphological analysis of the group (Buck *et al.* 2005) more or less supported the generic make-up of Callicostaceae, and placed *Pilotrichum* in its own subfamily.

The Pilotrichaceae are treated here as a monogeneric family that occupies a transitional position between the families traditionally placed in the Hookeriales and the Leucodontales. The uniqueness of the Pilotrichaceae is supported by the following constellation of characters that seems to span the Hookeriales-Leucodontales families: creeping, sympodially branched stolons; weakly and irregularly branched rhizoids from clusters of initials abaxial to the stolon leaf insertions; filamentous to subfoliose pseudoparaphyllia; stipitate-frondose habit; stems with a hyalodermis but no central strand; 2-celled axillary hairs; leaf cells small, thick-walled, often unipapillose; alar cells absent or weakly differentiated; costae double, long, strong, often with a dorsal crest and with dorsal propagula; setae short; exothecial cells thick-walled; peristome with narrow, completely papillose exostome teeth; endostome segments flat, cilia absent or rudimentary; calyptrae mitrate and having archegonia remnants as well as multiseriate hairs.

Buck (1987, 1998) viewed the most morphologically reduced members of *Pilotrichum* as the basal members of the genus. On the basis of this interpretation, he considered *Pilotrichum* phylogenetically close to *Callicostella*. The opposite view is taken here, and the morphologically complex species, especially those with well-developed stolons and stipitate-frondose habit, are considered the basal members of the genus, thus relating the group to the Leucodontales.

1. *Pilotrichum* P. Beauv., Mag. Encycl. 5: 327. 1804. *Neckera* subgen. *Pilotrichum* (P. Beauv.) Chevall., Fl. Gén. Env. Paris 2: 71. 1827. *Daltonia* sect. *Pilotrichum* (P. Beauv.) Arn., Mém. Soc. Linn. Paris 5: 295. 1826.

Hookeria sect. *Scleroneuron* Hampe, Linnaea 20: 96. 1847.
Callicosta Müll. Hal., Linnaea 21: 188. 1848.
Eupilotrichum Müll. Hal., Bull. Herb. Boissier 5: 205. 1897, invalid name.

Plants medium-sized to large, sometimes slender and wiry, yellow red, yellow green, green, or pale green. Stolons creeping; leaves appressed to spreading; rhizoids smooth, reddish brown, from clusters of initials abaxial to the leaf insertions, on stolons, and at the base of primary stems. Stems erect to pendent, often stipitate, regularly pinnately to bipinnately branched; branches determinate or indeterminate, evenly foliate; stems in cross section with sclerodermis well developed (a unistratose hyalodermis sometimes present), cortical cells enlarged, firm- to thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia narrowly foliose to filamentous. Stipe leaves distantly spaced, appressed or appressed below and squarrose above, ovate, ovate-triangular, oblong-triangular to triangular; margins often narrowly recurved. Stem and branch leaves erect-incurved to catenulate, erect-flexuose, or erect-appressed when dry, smooth or undulate to rugose. Stem leaves ovate, broadly ovate, oblong, or ovate-triangular, acute, rounded-acute, or obtuse, decurrent; margins subentire, serrulate, or serrate, plane above or recurved, at times bordered by elongate to sigmoid cells; costae strong, double, reaching above midleaf, often subpercurrent, parallel or diverging throughout, dorsal crest present or absent, usually ending in a stout tooth; cells smooth or prorate, oval, elliptic, oblong, or sigmoid, thick-walled, occasionally porose, subapical cells sometimes longer than surrounding cells; alar cells not or weakly differentiated, cells across the insertions reddish, porose. Branch leaves ovate, broadly ovate, or elliptic, acute or obtuse and mucronate, at times galeate, decurrent; margins serrulate or subentire, plane, inflexed or incurved; costae strong, double, ending above midleaf, often subpercurrent, dorsal crest present or absent, usually ending in a stout tooth; cells smooth, prorate or papillose, oval to oblong, thick-walled, occasionally porose; alar cells not or weakly differentiated. Asexual propagula often present on upper, dorsal surface of the costae, at the base of the costae, or on leaf margins. Dioicous, synoicous, or autoicous. Perichaetia and perigonia on short lateral branches; perichaetial leaves lanceolate, costae strong and double. Setae short, flexuose, smooth or roughened above. Capsules exserted or immersed, erect, oblong-cylindric, symmetric; exothecial cells thick-walled; stomata usually present; opercula short-rostrate; annuli rudimentary; peristome diplolepideous; exostome teeth pale yellow, narrowly triangular, dorsal (outer) surface papillose throughout, trabeculae and median line faint; endostome yellow, lightly papillose throughout, basal membranes low, segments not or narrowly perforate, not keeled, cilia rudimentary or absent. Calyptrae mitrate, with sparse hairs and/or archegonia.

Pilotrichum is a genus of 20 species restricted to the American tropics. The genus is remarkable in having four distinct, non-overlapping distributional patterns: Greater Antillean (5 species); Lesser Antillean (5 species); Central America–northern South America (5 species); and Cocos Island (2 species). Only *P. bipinnatum*, *P. fendleri*, and *P. evanescens* are broadly distributed throughout the range of the genus. There has been controversy over whether *Pilotrichum* or *Callicosta* is the proper name for this genus. The nomenclatural confusion surrounding the genus involved past interpretations of Article 63 of the *International Code of Botanical Nomenclature* (see Buck 1998). It has now been determined that *Pilotrichum* is the correct name for the genus.

In aspect, *Pilotrichum* is remarkably distinct and can be recognized in the field because of its usually frondose-stipitate habit and regularly pinnate to bipinnately branched stems with evenly foliate leaves. The stems and branches have a very thick sclerodermis, no central strand, and branch and stem buds surrounded by filamentous to subfoliose pseudoparaphyllia. The leaves of *Pilotrichum* can have four distinct morphologies: stolon, stipe, stem, and branch. Central American plants of *Pilotrichum* have two basic aspects when dried. In one the leaves are erect-incurved to catenulate (*P. andersonii*, *P. bipinnatum*, *P. fendleri*), while in the other the leaves are erect to erect-appressed (*P. asperifolium*, *P. corrugatum*, *P. evanescens*, *P. ramosissimum*, *P. rugifolium*). The leaf cells, with few exceptions, are

small and thick-walled, they may be smooth or strongly prorate, and alar cells are poorly developed or absent. The leaf costae are double, very strong, often ending near the apex and can be dorsally crested or have distinct dorsal teeth. Most species of *Pilotrichum* produce leaf propagula, and the Central American species can be placed into three groups depending on propagulum position: upper dorsal side of costae (*P. andersonii*, *P. corrugatum*, *P. fendleri*, *P. ramosissimum*); upper dorsal side of costae and leaf margin (*P. asperifolium*); and base of costae (*P. evanescens*, *P. rugifolium*). One species (*P. bipinnatum*) lacks leaf propagula.

The sporophytes within *Pilotrichum* are remarkably uniform. All species have short setae; erect, oblong-cylindric, symmetric capsules; thick-walled exothecial cells; and short-rostrate opercula. *Pilotrichum* species have a diplolepideous peristome with narrow, pale yellow exostome teeth that are papillose throughout. They have a reduced endostome with a low basal membrane, narrow, flat segments, and rudimentary or absent cilia. The calyptrae in all *Pilotrichum* species are mitrate and covered with archegonia and/or multiseriate hairs.

Crosby (1969a) revised *Pilotrichum*, and he tentatively placed the genus near *Helicoblepharum* on the basis of similarity in peristome structure, leaf areolation, and calyptral morphology. Buck (1998) treated the thirteen West Indian *Pilotrichum* species. He considered the genus near *Callicostella* on the basis of similarity in their stem anatomy, axillary hairs, and calyptral morphology.

The name *Pilotrichum* combines the Greek *pilos* (equivalent to the Latin *pileus*, a felt, mitrate cap) and Greek *trichum* (equivalent to the Latin *pilosus* hairy, with distinct long ascending hairs), and it refers to the hairy mitrate calyptrae of the genus.

1. Branch leaves conspicuously rugose; plants endemic to Cocos Island 2
1. Branch leaves not rugose or occasionally weakly undulate; plants present on mainland Central America 3

2. Stem and primary branch leaves bordered below by 3–6 rows of elongate cells; costae long, 0.8–0.9 the length of the leaves; stipe leaves squarrose when wet, ovate-triangular; propagula on dorsal surface at apex of costae; capsules exserted . . . . . 4. *P. corrugatum*
2. Leaves not bordered by elongate cells; costae short, 0.6–0.8 the length of the leaves; stipe leaves erect-spreading when wet, ovate; propagula on dorsal surface at base of costae; capsules immersed . . . . . 8. *P. rugifolium*

3. Costae short, 1/2–3/4 the length of the leaves. . . . . 5. *P. evanescens*
3. Costae long, exceeding 3/4 the length of the leaves 4

4. Plants producing indeterminate primary branches at regular intervals, most vertical growth from indeterminate primary branches. . . . . 7. *P. ramosissimum*
4. Plants rarely producing indeterminate branches, most vertical growth from elongation of stems 5

5. Subapical branch leaf cells 12–20 µm long 6
5. Subapical branch leaf cells 6–10 µm long 7

6. Plants synoicous; propagula absent; setae 1–1.7 mm long . . . . . 3. *P. bipinnatum*
6. Plants dioicous; propagula often present on upper, dorsal surface of the costa; setae 1.5–2.5 mm long . . . . . 6. *P. fendleri*

7. Leaves erect-catenulate when dry; margins minutely serrulate to subentire; when present dorsal costal crests 1 cell high, present only at apex; propagula near the costal apex . . . . . 1. *P. andersonii*
7. Leaves erect to erect-appressed when dry; margins usually serrate, but often notched due to propagulum loss; dorsal costal crest 1–3 cells high, often extending along 2/3 of the costae; propagula on margins and near the costal apex . . . . . 2. *P. asperifolium*

1. *Pilotrichum andersonii* Crosby, Bryologist 72: 296. 1969. *Callicosta andersonii* (Crosby) Crosby, Bryologist 81: 436. 1978. Protologue. *Crosby 2303*, Trinidad, trail up El Tocuche, Northern Range. Type. Trinidad. County of St. George: Northern Range. Trail to El Tocuche from Acono

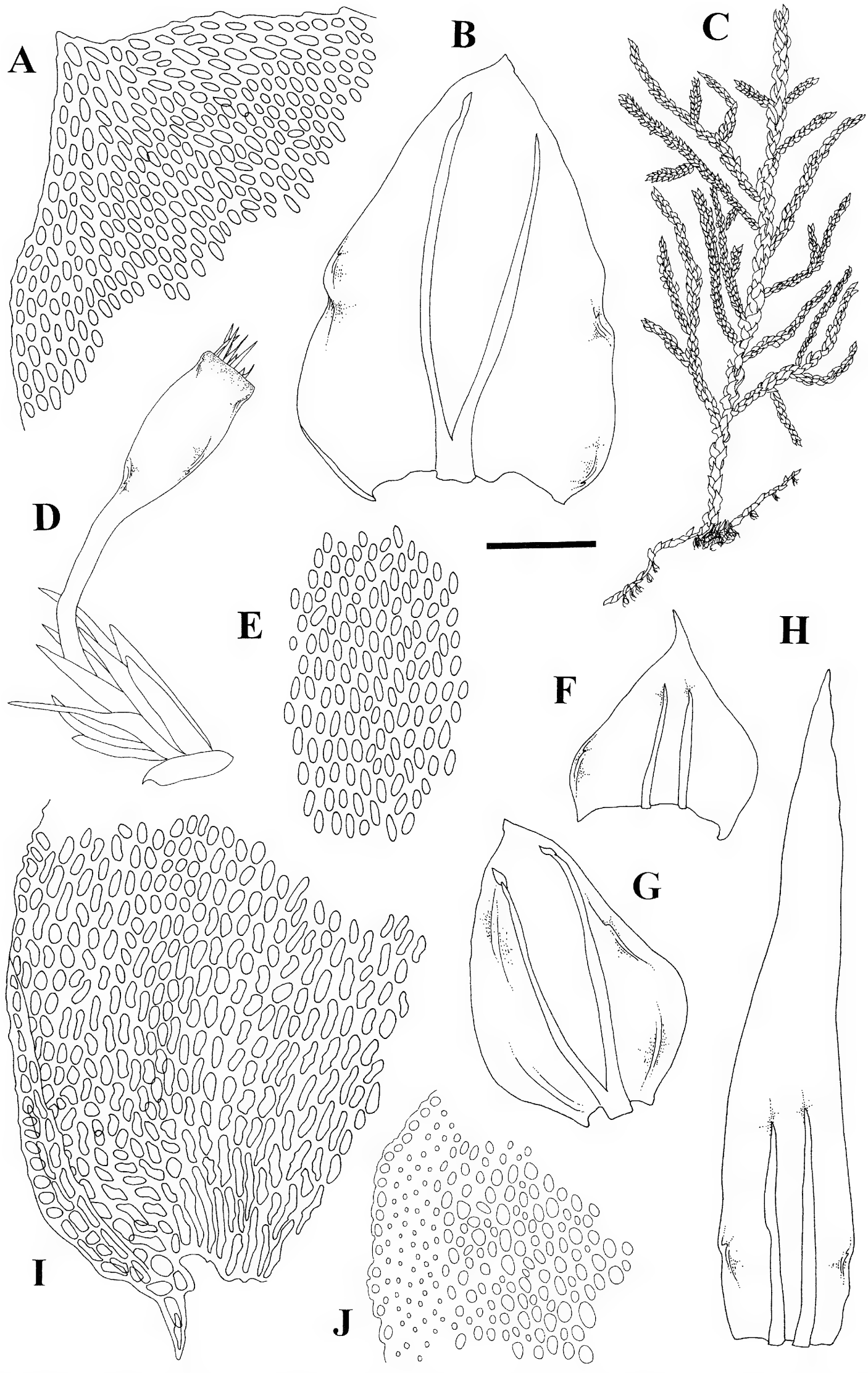
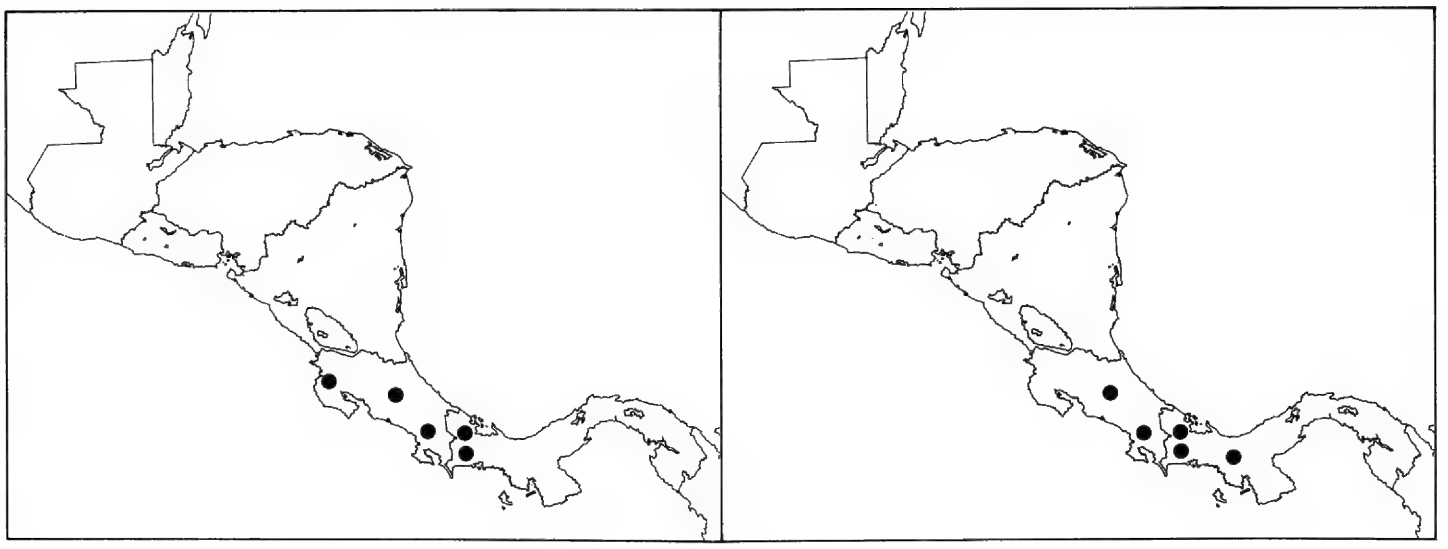


Figure 120. *Pilotrichum andersonii*. A. Leaf apex. B. Stem leaf. C. Habit. D. Seta and capsule. E. Median leaf cells between the costae. F. Stipe leaf. G. Branch leaf. H. Perichaetial leaf. I. Basal and alar cells. J. Stem in cross section. Scale in mm: bar = 0.05 (A, E, I); bar = 0.08 (J); bar = 0.20 (F, H); bar = 0.28 (B, G); bar = 0.9 (D); bar = 5.0 (C). B, D, G from *Crosby 2303* (type); all other figure parts from *Allen 5793*.



Pilotrichum andersonii *Pilotrichum asperifolium*

Road, north of St. Joseph. Altitude 1500–1700 feet, *M. R. Crosby No. 2303*, 23 July 1965 (MO, isotype).

Pilotrichum bipinnatum (Schwägr.) Brid. var. *filinerve* Müll. Hal., Syn. Musc. Frond. 2: 178. 1851. Protologue. In insula Trinidad, ubi in monte Tocuche sterilem legit *Crüger* 1847. 14 Mart.

Plants medium-sized, 4–7 cm long, yellow green to pale green. Stolons creeping; leaves appressed to spreading, oblong-triangular, 0.4–0.6 mm long, costae strong and double, dark red across the leaf insertions; rhizoids smooth, reddish brown, from clusters of initials abaxial to the leaf insertions, densely present on stolons, and at the base of primary stems. Stems erect to pendent, regularly pinnately to bipinnately branched, evenly foliate; stems in cross section with unistratose hyalodermis, subsclerodermis of 3–6 rows of small, very thick-walled, red cells, cortical cells enlarged, firm- to thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia narrowly foliose to filamentous. Stem and branch leaves erect-incurved or catenulate when dry, erect-spreading when wet. Stem leaves ovate to ovate-triangular, 0.8–1.2 mm long, acute to rounded-acute, narrowly decurrent; margins minutely serrulate at apex, or subentire throughout, plane above, recurved at base; costae strong, double, reaching 0.8–0.9 the leaf length, not crested or crest low (one cell high) and confined to the uppermost part, irregularly toothed in upper 1/2, stoutly toothed at apex; cells smooth or inconspicuously prorate, oval to oblong, 4–15 µm long, thick-walled, occasionally porose; alar cells not or weakly differentiated, cells across the insertions reddish, porose. Branch leaves ovate to broadly ovate, acute or obtuse and mucronate at the apex, 0.5–1.0 mm long, narrowly decurrent; margins minutely serrulate at apex, or subentire throughout, plane above, reflexed at base; costae strong, double, reaching 0.8–0.95 the leaf length, not crested or crest low (1–3 cells high), confined to the uppermost part, irregularly toothed in upper 1/2, stoutly toothed at apex; cells smooth or inconspicuously prorate, oval to oblong, 4–18 µm long, thick-walled, occasionally porose; alar cells not or weakly differentiated, cells across the insertions reddish, porose. Asexual propagula occasionally present on upper, dorsal surface of the costae. Dioicous. Perichaetia and perigonia on short lateral branches on stems and branches; perigonial leaves ovate-lanceolate, 0.8–1.0 mm long, perichaetial leaves lanceolate, 1.0–1.2 mm long, in both costae strong and double. Setae short, flexuose, 1.5–2.0 mm, smooth. Capsules exserted, erect, oblong-cylindric, symmetric, 1.0–1.2 mm long; exothecial cells dark red, oblate in 3–5 rows at mouth, those below short-rectangular, thick-walled; stomata on neck; operculum not seen; annulus not seen; peristome diplolepideous; exostome teeth pale yellow, narrowly triangular, 0.3–0.5 mm long, dorsal surface papillose throughout, trabeculae and median line faint; endostome yellow, lightly papillose throughout, basal membranes low, segments subulate, not or narrowly perforate, not keeled, cilia rudimentary. Spores rounded to irregularly oblong, 14–26 µm, lightly papillose. Calyptra not seen.

Illustrations. Crosby (1969a, Figs. 36–42, 176). Figure 120.
Habitat. On tree trunks, branches, and rotting logs; 475–1400 m.

Distribution in Central America. COSTA RICA. Cartago: *Townsend 93/145* (MO); Guanacaste: *Crosby 3832B* (MO); Puntarenas: *Walter James* (US, mixed with *P. asperifolium*). PANAMA. Bocas del Toro: *Allen 5793* (MO); Chiriquí: *Folsom et al. 5351* (MO).

World range: Central America; Caribbean (Trinidad and Tobago), Northern and Western South America.

Pilotrichum andersonii is a medium-sized species, with mostly ovate stem and branch leaves that are erect-incurved to catenulate when dry. Its leaves have subentire to minutely serrulate margins that are recurved or reflexed at the base, and long costae that although stoutly toothed above have only a slight hint of a dorsal crest. The leaf cells are oval to oblong, mostly smooth, and thick-walled. Sporophytically, *P. andersonii* has short, flexuose setae and exserted capsules. Most Central American collections of *P. andersonii* lack leaf propagula, but when present the propagula are found at or near the tip of the costae.

Pilotrichum asperifolium and *P. fendleri* are the only Central American species likely to be confused with *P. andersonii*. All three species are similar in size, leaf shape, costal length, and leaf cell shape. *Pilotrichum asperifolium*, however, has short, indeterminate branches and its leaves are erect to erect-appressed when dry rather than erect-catenulate. Furthermore, its leaves have serrate margins, often conspicuously papillose cells, and often strongly developed, toothed, dorsal costal crests 1–3 cells high. When propagula are present in *P. asperifolium* they are found dorsally at the apex of the costae and along the leaf margins. Lastly, the older leaves in *P. asperifolium* often have notched margins that mark the previous points of attachment of marginal leaf propagula. *Pilotrichum andersonii* and *P. fendleri* both have leaves that are erect-catenulate when dry, costae with narrow dorsal crests, and propagula near the costal apex. *Pilotrichum fendleri*, however, has longer apical branch leaf cells between the tips of costae (12–20 µm vs. 6–10 µm).

2. *Pilotrichum asperifolium* Mitt., J. Linn. Soc., Bot. 12: 387. 1869. *Callicosta asperifolia* (Mitt.) Crosby, Bryologist 81: 436. 1978. Protologue. [Colombia] Hab. Andes Bogotenses, Montaña fluvii Sogamoza, etiam in montibus prope Bucaramanga (6500 ped.), ad arborum truncos, *Weir, n. 148*. Type. Musci Novae Granatenses. Andes Bogotensis. Alt. 6500′, *J. Weir No. 148* (US, isotype).

Plants medium-sized, 3–7 cm long, yellow green to pale green. Stolons creeping; leaves appressed to spreading, oblong-triangular, 0.4–0.6 mm long, costae strong and double, dark red across the leaf insertions; rhizoids smooth to lightly roughened, reddish brown, from clusters of initials abaxial to the leaf insertions, on stolons, and at the base of primary stems. Stems erect to pendent, regularly pinnately to bipinnately branched, evenly foliate; stems in cross section often with a row of somewhat enlarged hyalodermis cells, subsclerodermis of 3–6 rows of small, very thick-walled, red cells, cortical cells enlarged, thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia narrowly foliose to filamentous. Branches determinate or indeterminate. Stem and indeterminate primary branch leaves erect to erect-appressed when dry, erect-spreading when wet, ovate, broadly ovate, oblong, or ovate-triangular, 0.8–2.0 mm long, acute to obtuse, narrowly decurrent; margins serrate, plane above, recurved at base; costae strong, double, reaching 0.8–0.9 the leaf length, often crested, crest 1–3 cells high, variably developed, at times extending 2/3 the costae length, at times irregularly toothed at apex; cells conspicuously or inconspicuously papillose, oval to narrowly oblong, 8–18 µm long, thick-walled, occasionally porose; alar cells not or weakly differentiated, cells across the insertions elongate, often reddish, porose. Determinate branch leaves elliptic to ovate, acute or obtuse and mucronate at the apex, 0.6–1.0 mm long, narrowly decurrent; margins serrate, plane above, reflexed at base; costae strong, double, reaching 0.8–0.95 the leaf length, crested, crest 1–3 cells high and toothed along upper margins; cells conspicuously papillose, oval to oblong, 9–16 µm long, thick-walled, occasionally porose; alar cells not or weakly differentiated, cells across the insertions reddish, porose. Asexual propagula on upper, dorsal surface of the costae and along the leaf margins. Dioicous. Perichaetia and perigonia on short lateral branches on stems and branches. Setae short, flexuose, 0.8–1.2 mm, smooth. Capsules exserted, erect, oblong-cylindric, symmetric, 1.0–1.2 mm long; exothecial cells dark red, oblate in 3–5 rows at mouth, those below short-rectangular, thick-walled; stomata on neck; opercula conic-rostrate, 0.5 mm long; annuli of several rows of enlarged,

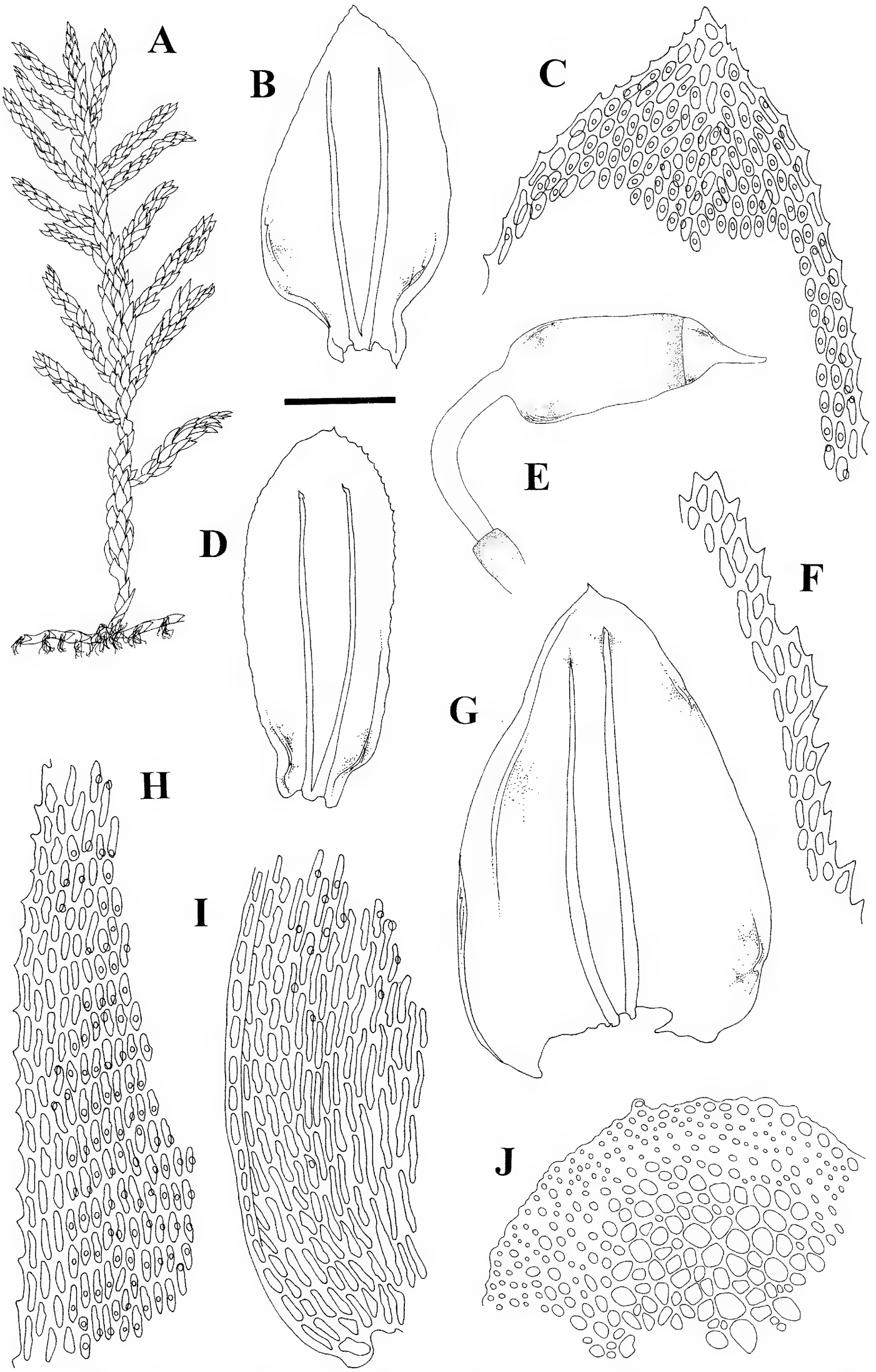


Figure 121. *Pilotrichum asperifolium*. A. Habit. B. Branch leaf. C. Leaf apex. D. Indeterminate branch leaf. E. Seta, capsule, and operculum. F. Dorsal costal crest. G. Stem leaf. H. Median leaf cells and margin. I. Basal and alar cells. J. Stem in cross section. Scale in mm: bar = 0.05 (C, F, H, I); bar = 0.08 (J); bar = 0.28 (B, D, G); bar = 0.8 (E); bar = 4.0 (A). B, E, G from *Crosby 13139*; J from *Crosby 3977*; all other figure parts from *Crosby 10291*.

deciduous cells; peristome diplolepideous; exostome teeth pale yellow, narrowly triangular, 0.3–0.5 mm long, dorsal surface papillose throughout, trabeculae and median line faint; endostome yellow, lightly papillose throughout, basal membranes low, segments subulate, not or narrowly perforate, not keeled, cilia rudimentary. Spores rounded to irregularly oblong, 12–18 µm, lightly papillose. Calyptrae mitrate, with archegonia and/or sparse hairs, 0.8–1.0 mm long.

Illustrations. Crosby (1969a, Figs. 76–81, 180). Figure 121.

Habitat. On trees and logs; 800–1768 m.

Distribution in Central America. COSTA RICA. Cartago: *Townsend 93/213* (MO); Puntarenas: *Crosby 13139* (CR, MO). PANAMA. Bocas del Toro: *Allen 5858* (MO); Chiriquí: *Crosby 3977* (MO); Veraguas: *Crosby 10291* (MO).

World range: Central America; Western South America.

Pilotrichum asperifolium is a medium-sized species with mostly ovate stem and branch leaves that are erect to erect-appressed when dry. It often has indeterminate branches, but unlike the indeterminate branches of *P. ramosissimum* they are only occasionally branched and do not significantly contribute to the vertical growth of the plants. Its leaves have serrate margins that are recurved or reflexed at the base and long costae that often have well-developed, toothed dorsal crests (1–3 cells high). Development of the dorsal costal crests in *P. asperifolium* varies from extending two-thirds the costal length to absent. The leaf cells are oval to narrowly oblong, often conspicuously papillose, and thick-walled. The sporophytes of *P. asperifolium* have short, flexuose setae, conic-rostrate opercula, and exserted capsules. Most Central American collections of *P. asperifolium* have propagula on the upper parts of the costae as well as along the leaf margins. When the marginal leaf propagula detach they leave behind deep notches in the margins, and older leaves that lack propagula commonly have notched margins.

Pilotrichum andersonii is the only Central American species likely to be confused with *P. asperifolium*. The species are similar in size, leaf shape, costal length, and leaf cell shape. *Pilotrichum andersonii*, however, lacks indeterminate branches and its leaves are often erect-catenulate when dry. Furthermore, its leaves have minutely serrulate to subentire margins, smooth or lightly papillose cells, and weakly developed dorsal costal crests only one cell high. More often than not the costae are only toothed at the apex. When propagula are present in *P. andersonii* they are found only dorsally at the apex of the costae.

3. *Pilotrichum bipinnatum* (Schwägr.) Brid., Muscol. Recent. Suppl. 4: 140. 1819. *Neckera bipinnata* Schwägr., Sp. Musc. Frond. Suppl. 1(2): 156. 1816. *Daltonia bipinnata* (Schwägr.) Arn., Mém. Soc. Hist. Nat. Paris 2: 303. 1826. *Hookeria bipinnata* (Schwägr.) Spreng., Syst. Veg. 4: 197. 1827. *Callicosta bipinnata* (Schwägr.) Müll. Hal., Linnaea 21: 188. 1848. Protologue. [French Guiana] In arboribus Guyanae legit cl. *Richard*.

Plants medium-sized, 3–12 cm long, reddish yellow, yellow green, or pale green. Stolons creeping; rhizoids smooth, reddish brown, from clusters of initials abaxial to the leaf insertions, on stolons, and at the base of primary stems. Stems erect to pendent, regularly bipinnately branched, evenly foliate; stems in cross section with unistratose hyalodermis, subsclerodermis of 5–8 rows of small, very thick-walled, red cells, cortical cells enlarged, firm- to thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia narrowly foliose to filamentous. Stipe leaves appressed when wet or dry, oblong-triangular to triangular, 1.0–1.4 mm long; margins narrowly recurved throughout; costae strong and double, dark red across the leaf insertions. Stem and branch leaves erect-incurved or catenulate when dry, erect-spreading when wet. Stem leaves ovate to ovate-triangular, 0.7–1.2 mm long, acute to rounded-obtuse, decurrent; margins minutely serrulate at apex or subentire throughout, plane above, recurved at base; costae strong, double, reaching 0.8–0.9 the leaf length, more or less parallel throughout, not crested, stoutly toothed at apex; cells smooth or inconspicuously prorate, oval, oblong to sigmoid, 6–15 µm long, thick-walled, not porose; alar cells not or weakly differentiated, cells across the insertions reddish, porose. Branch leaves elliptic to broadly ovate, acute to broadly apiculate at the apex, 0.6–1.0 mm long, narrowly decurrent; margins minutely serrulate at apex, or subentire throughout, plane above, reflexed at base; costae strong, double, reaching 0.8–0.95

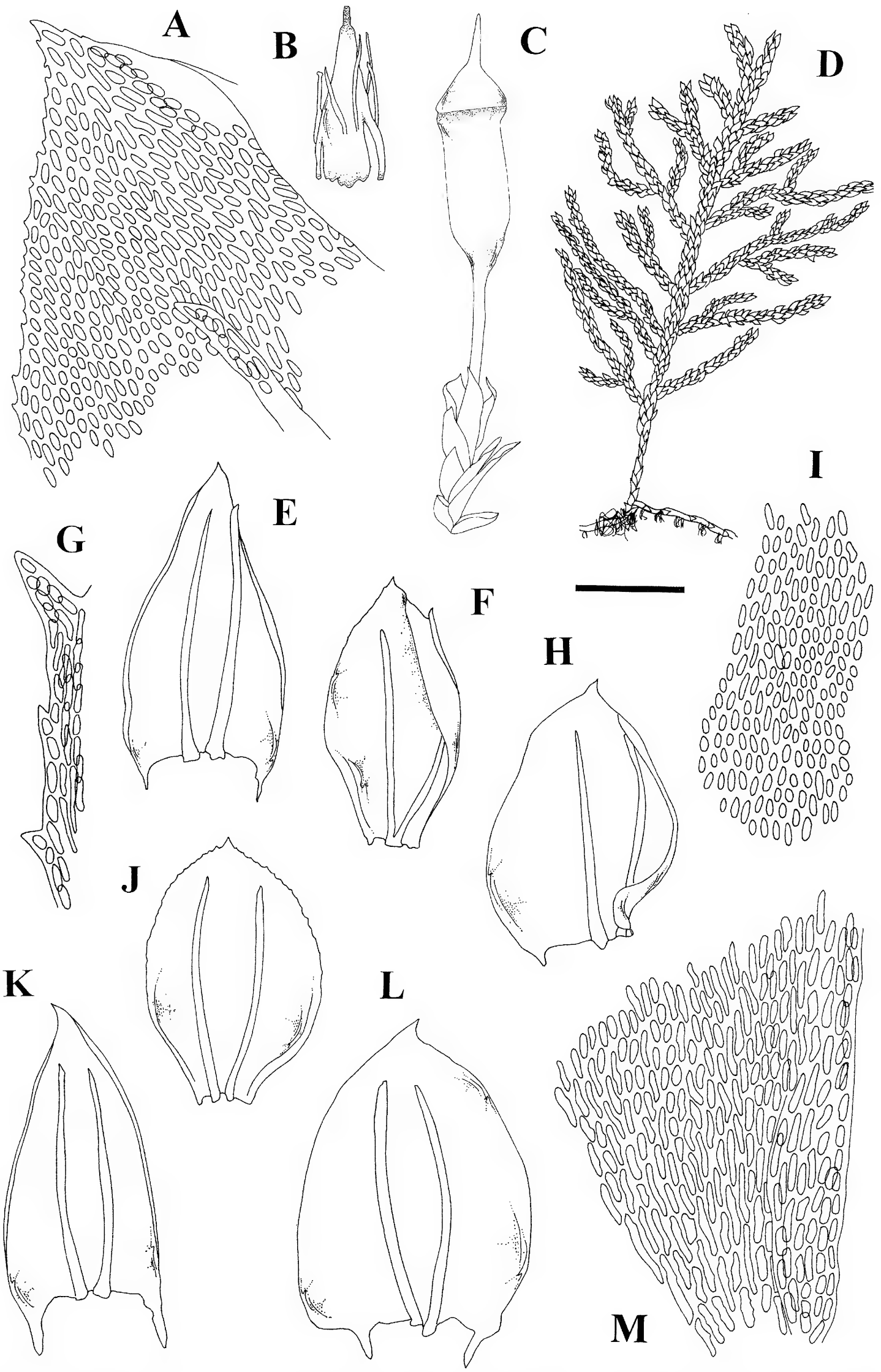
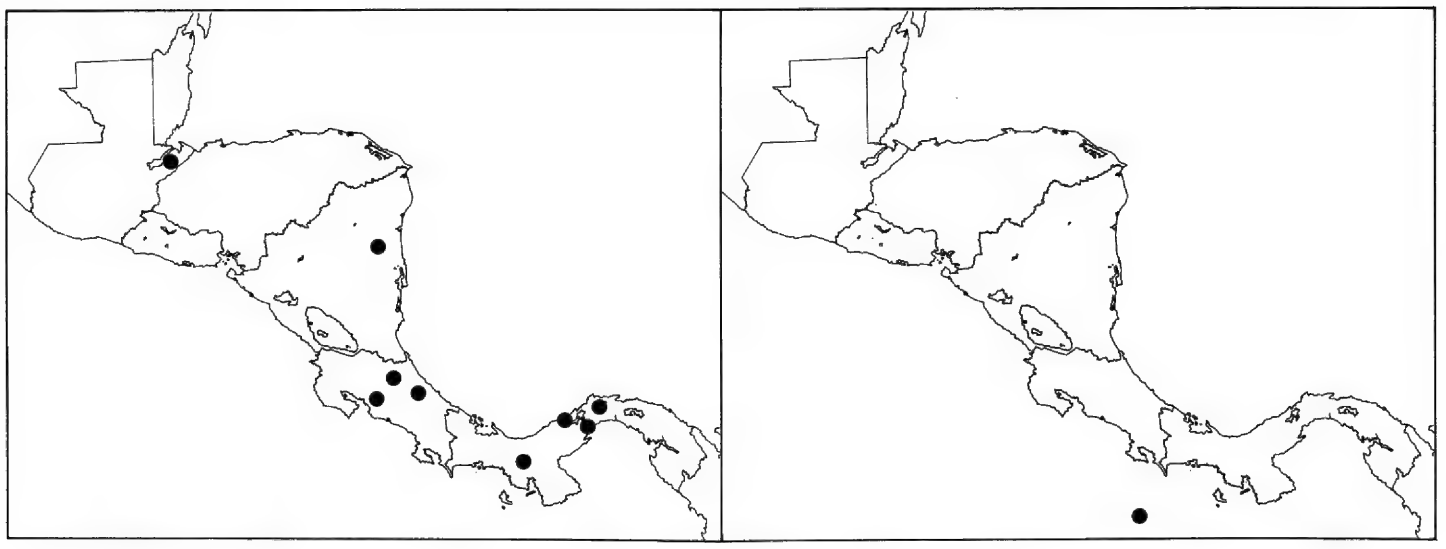


Figure 122. *Pilotrichum bipinnatum*. A. Leaf apex. B. Calyptra. C. Seta, capsule, and operculum. D. Habit. E & K. Stipe leaves. F & J. Branch leaves. G. Dorsal costal crest. H & L. Stem leaves. I. Median leaf cells between the costae. M. Basal and alar cells. Scale in mm: bar = 0.05 (A, G, I, M); bar = 0.28 (F, J); bar = 0.5 (E, H, K, L); bar = 0.6 (B); bar = 0.8 (C); bar = 6.4 (D). D from *Crosby 10423*; E, K from *Crosby 10897*; all other figure parts from *Grayum 10008*.



Pilotrichum bipinnatum *Pilotrichum corrugatum*

the leaf length, more or less parallel throughout, not crested, stoutly toothed at apex; cells smooth or inconspicuously prorate, round to narrowly elliptic, 4–22 µm long, thick-walled, occasionally porose; alar cells not or weakly differentiated, cells across the insertions reddish, porose. Asexual propagula unknown. Synoicous or autoicous. Inflorescences on short lateral branches on stems and branches; perichaetial leaves lanceolate, 0.6–1.1 mm long. Setae short, flexuose, 1.0–1.7 mm, smooth. Capsules exserted, erect, oblong-cylindric, symmetric, 1–2 mm long; exothecial cells dark red, oblate in 3–5 rows at mouth, those below short-rectangular, thick-walled; stomata on neck; opercula short-rostrate, 0.6–1.0 mm long; annuli rudimentary; peristome diplolepideous; exostome teeth pale yellow, narrowly triangular, dorsal surface papillose throughout, trabeculae and median line faint; endostome yellow, lightly papillose throughout, basal membranes low, segments subulate, not or narrowly perforate, not keeled, cilia rudimentary. Spores rounded to irregularly oblong, 14–18 µm, lightly papillose. Calyptrae mitrate, with archegonia and/or sparse hairs, 0.5–0.8 mm long.

Illustrations. Bartram (1949, Fig. 130 G–I); Crosby (1969a, Figs. 87–95, 196–197); Florschütz-de Waard (1986, Fig. 116); Churchill and Linares (1995, Fig. 43 a–f); Buck (1998, Pl. 29 13, Pl. 35 6–11); Gradstein *et al.* (2001, Fig. 168 I–M); Buck (2003, Fig. 99). Figure 122.

Habitat. On vines, tree roots, trunks, branches, and twigs; 10–550(–1880) m.

Distribution in Central America. GUATEMALA. Izabal: *Steyermark 38188* (F, FH). NICARAGUA. Zelaya: *Proctor* 27232 (MO, NY). COSTA RICA. Heredia: *Grayum 10008* (MO); Limón: *Standley 36886* (FH, US); San José: *Holz & Schäfer-Verwimp CR 99-1306* (MO). PANAMA. Canal Area: *Maxon 4874* (NY, US); Colón: *Crosby 4443* (F, MO, US); Panamá: *Crosby 10423* (MO); Veraguas: *Crosby 10132* (MO).

World range: Central America; Caribbean; Western and Northern South America, Brazil.

Pilotrichum bipinnatum is found throughout Central America and is one of the most broadly distributed species in *Pilotrichum* (Crosby 1969a). It is medium-sized species with regularly bipinnate stems. It has a strongly stipitate habit, with well-differentiated stipe leaves that are erect-appressed, whether wet or dry, and have recurved margins. Its leaves are erect-catenulate when dry and decurrent; they have long costae that are more or less parallel throughout, lack dorsal crests, and end in a strong, forward-pointing tooth. The branch leaf cells vary from round to narrowly elliptic and have only a few short-rectangular cells at the basal angles. *Pilotrichum bipinnatum* has never been found with asexual propagula. An outstanding feature of *P. bipinnatum* is its synoicous sexual condition; it is the only species in *Pilotrichum* with this feature. There are occasional plants of *P. bipinnatum* that are autoicous rather than synioious. The setae of *P. bipinnatum* are variable in length both within and between collections, but the capsules are consistently exserted. The opercula are conic-rostrate, and the short, mitrate calyptrae bear archegonial remnants as well as sparse hairs.

Pilotrichum fendleri is very similar to *P. bipinnatum* in overall aspect, but it is a dioicous species. It further differs from *P. bipinnatum* in having propagula on its costae and longer setae (1.5–2.5 mm

vs. 1–1.7 mm). Buck (1998) found that Caribbean material of *P. fendleri* had ultimate branch leaves that were different in shape (oblong-ovate vs. ovate to obovate) from those of *P. bipinnatum*, and that *P. fendleri* had shorter cells between the costae than *P. bipinnatum* (less than vs. more than 14 µm). These distinctions, however, are not apparent in Central American material of *P. fendleri* and *P. bipinnatum*.

4. *Pilotrichum corrugatum* Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 41(1): 79. 1905. Protologue. [Costa Rica] Hab. Amer. centr. Pacifique: île Cocos (*H. Pittier*).

Pilotrichum obtusatum Williams, Bryologist 27: 38. 1924. Protologue. Cocos Island, [*Alban Stewart*] *1375*.

Plants medium-sized to large, 5–12 cm long, green, yellow green, or reddish yellow. Stolons creeping; rhizoids smooth to lightly roughened, reddish brown, from clusters of initials abaxial to the leaf insertions, on stolons, and at the base of primary stems. Stems erect to pendent, bipinnately branched, evenly foliate; stems in cross section with sclerodermis of 4–7 rows of small, very thick-walled, red cells, cortical cells enlarged, thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia narrowly foliose to filamentous; branches determinate. Stipe leaves distantly spaced, appressed at base, squarrose above, ovate-triangular, 1.4–1.7 mm long, long-decurrent; margins narrowly recurved throughout; costae strong and double, dark red across the leaf insertions, converging above, tips projecting as spines, at times weakly crested. Stem and primary branch leaves erect to erect-flexuose when dry, erect-spreading when wet, conspicuously rugose. Stem leaves narrowly ovate, 0.6–2.0 mm long, broadly acute to obtuse, decurrent; margins serrulate, plane above, narrowly recurved below; costae strong, double, reaching 0.8–0.9 the leaf length, at times weakly crested, crest one cell high, toothed at apex and with a few low teeth on the upper 1/3; cells obscurely papillose, irregularly positioned, upper cells isodiametric to narrowly oblong, 4–16 µm long, thick-walled, occasionally porose, marginal cells in basal half or throughout leaf elongate to sigmoid, 16–35 µm long; basal cells elongate, porose; alar cells not or weakly differentiated as irregularly triangular, porose cells. Primary branch leaves narrowly ovate, rounded-acute to obtuse, 1.0–1.5 mm long, decurrent; margins serrulate above, plane above, reflexed below; costae strong, double, reaching 0.8–0.95 the leaf length, at times crested, crest one cell high, toothed above, ending in a forward-pointing spine; cells papillose, oblong to narrowly oblong, 5–15 µm long, thick-walled, not porose; basal cells elongate, porose; alar cells not or weakly differentiated as a few rectangular cells. Asexual propagula on upper, dorsal surface of the costae. Dioicous. Perichaetia and perigonia on short lateral branches on stems and branches. Setae short, flexuose, 1–2 mm, smooth to lightly roughened, yellow when young, red when mature. Capsules exserted, erect, oblong-cylindric, symmetric, 1.0–1.5 mm long; exothecial cells dark red, oblate in 3–5 rows at mouth, those below short-rectangular, thick-walled; stomata rudimentary, on neck; opercula conic-rostrate, 0.5–1.0 mm long; annuli of several rows of enlarged, deciduous cells; peristome diplolepideous; exostome teeth whitish yellow, narrowly triangular, 0.3–0.5 mm long, dorsal surface papillose throughout, trabeculae and median line faint; endostome whitish yellow, lightly papillose throughout, basal membranes low, segments subulate, not or narrowly perforate, not keeled, cilia rudimentary. Spores rounded to irregularly oblong, 12–18 µm, lightly papillose. Calyptra not seen (mitrate, sparsely hairy, Williams 1924).

Illustrations. Williams (1924, Pl. 6); Crosby (1969a, Figs. 82–86, 184). Figure 123.
Habitat. On trees and logs; 200–300 m.
Distribution in Central America. COSTA RICA. Puntarenas, Cocos Island: *Gómez 4605* (FH, MO).
World range: Endemic to Cocos Island.

Pilotrichum corrugatum is a medium-sized to large species with long stems, well-spaced branches, and long, narrowly ovate, strongly rugose stem and branch leaves. It has a strongly stipitate habit, with exceptionally well-developed stipe leaves that are well spaced, squarrose above when wet, and have margins tightly recurved throughout. Its leaves are distinctly decurrent and have long costae that end in a prominent, forward-pointing tooth. The costae occasionally are weakly crested, with the crest only one cell high and restricted to the uppermost part of the costa. Leaf cell areolation in *P. corrugatum* is very irregular, perhaps due to its strongly rugose leaves. The interior cells vary from isodiametric to narrowly oblong, and the lower marginal cells (and sometimes the upper ones) are differ-

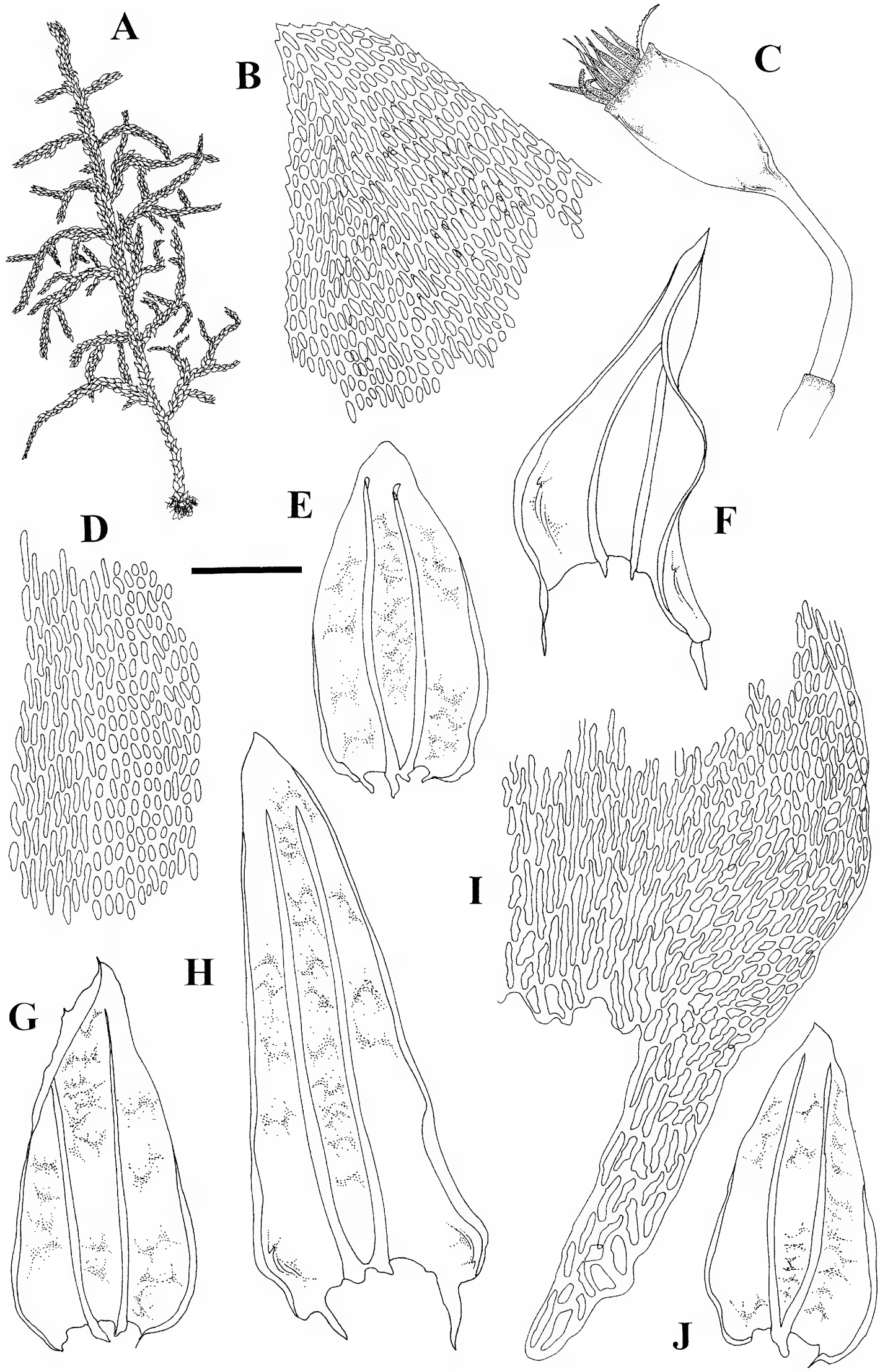


Figure 123. *Pilotrichum corrugatum*. A. Habit. B. Leaf apex. C. Seta and capsule. D. Median leaf cells near margin showing elongate border cells. E, G & J. Branch leaves. F. Stipe leaf. H. Stem leaf. I. Basal and alar cells. Scale in mm: bar = 0.06 (B, D, I); bar = 0.4 (E–H, J); bar = 1.25 (C); bar = 12.7 (A). All figure parts from *Gómez 4569*.

entiated into several rows of elongate to sigmoid cells that form a more or less distinct border. As noted by Crosby (1969a), the border is most obvious at midleaf because of the sharp contrast it makes with the shorter, irregularly arranged interior cells. When present, the asexual propagula of *P. corrugatum* are found on the upper, dorsal side of the costae. The sporophytes of *P. corrugatum* have short, flexuose setae, conic-rostrate opercula, and exserted capsules.

Pilotrichum rugifolium is the only Central American species likely to be confused with *P. corrugatum*. Both species are endemic to Cocos Island; they are similar in size, overall aspect, leaf shape, and in having strongly rugose leaves. *Pilotrichum rugifolium*, however, lacks well-differentiated stipe leaves, its leaves are not bordered by elongate to sigmoid cells, and it has short costae that extend only to 0.6–0.8 the leaf length. Crosby (1969a) noted the costae of *P. corrugatum* are parallel after diverging near the base of leaf, while those of *P. rugifolium* diverge slightly throughout their length. While this is true for the stem and branch leaves of *P. corrugatum*, its stipe leaves have costae that converge at the tips. Lastly, *P. rugifolium* has immersed capsules and propagula at the base of the costae, while *P. corrugatum* has exserted capsules and propagula at the apex of the costae.

Thamniopsis diffusa is often found mixed with collections of *Pilotrichum corrugatum*. Both species have strongly rugose leaves, and this makes them superficially similar. In fact, the MO specimen of Gradstein's, *Bryophyta Neotropica Exsiccata no. 372*, consists entirely of *Thamniopsis diffusa*. It differs from *P. corrugatum* in having a stem hyalodermis, more weakly differentiated double costae, and long, lax leaf cells.

5. *Pilotrichum evanescens* (Müll. Hal.) Crosby, Bryologist 72: 326. 1969. *Callicosta evanescens* Müll. Hal., Linnaea 21: 189. 1848. *Pilotrichum bipinnatum* (Schwägr.) Brid. var. *evanescens* (Müll. Hal.) Müll. Hal., Syn. Musc. Frond. 2: 179. 1851. Protologue. [Suriname] Bei Paramáribo (Tourtonne und Quarta) auf faulenden Baumstämmen. Hb. *Kegel. No. 742.*

Pilotrichum amazonum Mitt., J. Linn. Soc., Bot. 12: 387. 1869. Protologue. [Brazil] Fl. Amazon, Caripi, *Spruce, n. 702*; Santarém, *Spruce, n. 703*. Fl. Negro, S. Gabriel, *Spruce, n. 701*; Marabitanas, *Spruce, n. 704.*
Pilotrichum dubium Mitt., J. Linn. Soc., Bot. 12: 390. 1869. Protologue. Ins. Guadelupe [sic], Herb. Hooker.
Pilotrichum trinitense Mitt., J. Linn. Soc., Bot. 12: 390. 1869. Protologue. Ins. Trinidad, ad Maraccas et Cheguanas, *Black.*
Pilotrichum cryphaeoides Besch., Ann. Sci. Nat., Bot., sér. 6. 3: 219. 1876. Protologue. Guadeloupe (*L'Herminier*). – Martinique, camp Balata (Husnot, *exsicc. n. 158*). Antilles (*Perrotet*).
Pilotrichum scabridum Broth., Hedwigia 45: 279. 1906. Protologue. [Brazil] Estado de Amazonas: Rio Madeira, an Zweigen am Marmellos [*Ule*] (*n. 2348*). Type. Amazonas-Expedition. An Zweigen, Wasserfülle des Marmellos. Rio Madeira: März 1902, *E. Ule 2348* (FH, isotype).
Pilotrichum spiculiferum E. B. Bartram, Rhodora 36: 57. 1934. Protologue. On tree trunk, Mocá, Dept. of Soloa, Guatemala, April, 1931, *J. Bequaert No. 68*. Types. Guatemala. On tree trunk, Moca (Guatalon), *J. Bequaert No. 68* (FH, holotype; F, isotype).

Plants medium-sized, 2–8 cm long, green, yellow green, or reddish yellow. Stolons creeping; rhizoids smooth to lightly roughened, reddish brown, from clusters of initials abaxial to the leaf insertions, on stolons, at base of primary stems, and stems and branches where they are in contact with the substrate. Stems erect to pendent, pinnately or bipinnately branched; branches determinate, evenly foliate; stems in cross section with sclerodermis of 4–7 rows of small, very thick-walled, red cells, cortical cells enlarged, thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia narrowly foliose to filamentous. Stipe leaves closely spaced, erect to erect-spreading when wet, ovate, 0.8–1.0 mm long, long-decurrent; margins narrowly recurved throughout; costae weak and double, 0.5–0.7 the leaf length, dark red across the leaf insertions, diverging throughout, tips occasionally projecting as spines. Stem and primary branch leaves erect when dry, erect-spreading, often in distinct ranks when wet, smooth or slightly rugose. Stem leaves narrowly or broadly ovate, 1.0–1.6 mm long, acute to broadly acute, decurrent; margins serrulate and plane above, subentire and narrowly recurved below; costae weak, double, diverging throughout, reaching 0.5–0.8 the leaf length, not crested, toothed at apex; cells strongly papillose to nearly smooth, upper cells elliptic to oblong, 8–25 µm long, thick-walled, occasionally porose, marginal cells similar to the interior cells; basal cells elongate, porose; alar cells weakly differentiated, quadrate to short-rectangular, at times porose. Primary branch leaves elliptic to ovate, acute to rounded-acute, apices often galeate, 1.0–1.4 mm long, decur-

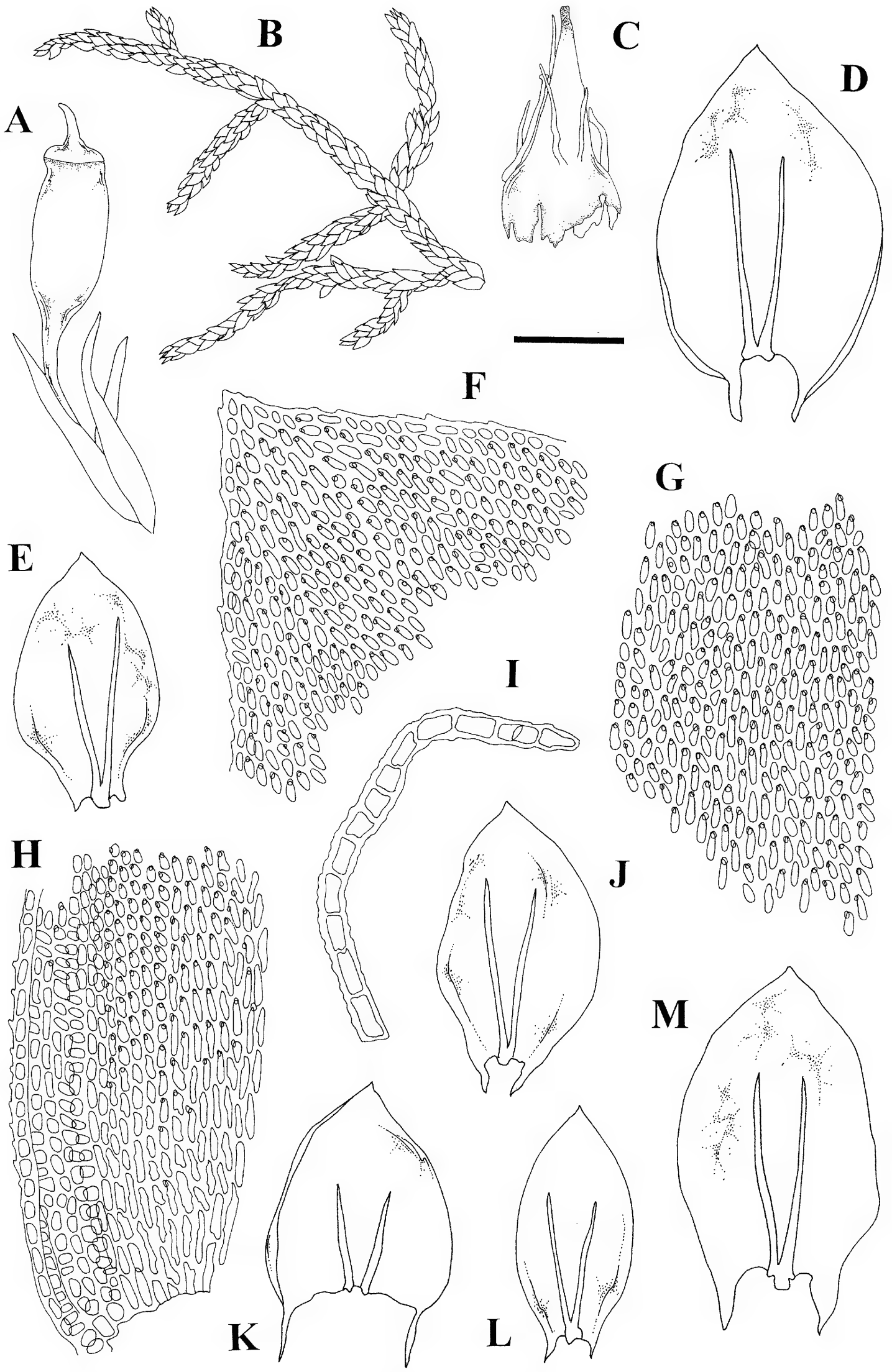
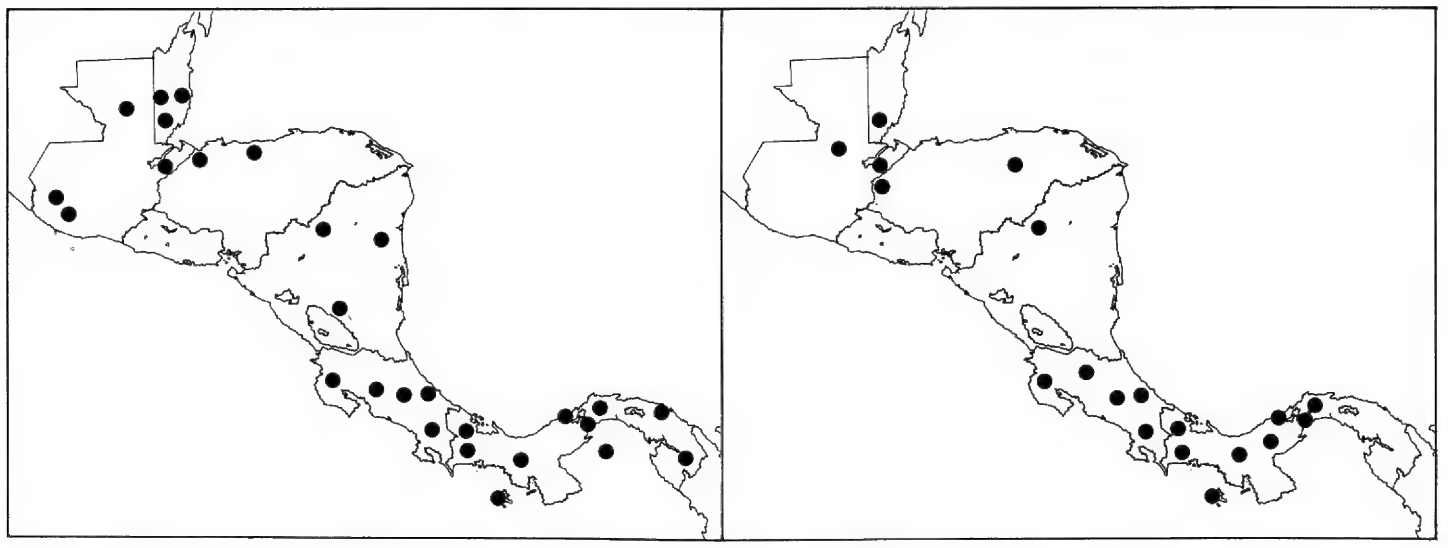


Figure 124. *Pilotrichum evanescens*. A. Seta, capsule, and operculum. B. Habit. C. Calyptra. D & M. Stem leaves. E, J & L. Branch leaves. F. Leaf apex. G. Median leaf cells between the costae. H. Basal and alar cells. I. Pseudoparaphyllum. K. Stipe leaf. Scale in mm: bar = 0.06 (F–I); bar = 0.4 (D, E, J–M); bar = 0.51 (C); bar = 0.9 (A); bar = 3.2 (B). A, C from *Alfaro 103*; all other figure parts from *Allen 18888*.



Pilotrichum evanescens *Pilotrichum fendleri*

rent; margins serrulate above, serrulate to subentire below, plane above, reflexed below; costae double, reaching 0.5–0.8 the leaf length, at times crested, crest one cell high, toothed above, ending in a forward-pointing spine; cells papillose to smooth, upper cells narrowly elliptic to oblong, 8–25 µm long, thick-walled, occasionally porose; basal cells elongate, porose; alar cells not or weakly differentiated as a few rectangular cells. Asexual reproduction by uniseriate, papillose-roughened propagula on dorsal surface at base of costae. Dioicous. Perichaetia and perigonia on short lateral branches on stems and branches. Setae short, 0.6–1.4 mm long, thickened at base, roughened, flexuose, red. Capsules exserted, erect, oblong-cylindric, symmetric, 1.5–2.0 mm long; exothecial cells dark red, oblate in 3–5 rows at mouth, those below subquadrate to short-rectangular, firm-walled; stomata immersed on neck; opercula conic-rostrate, 0.5 mm long; annuli of several rows of enlarged, thick-walled, deciduous cells; peristome diplolepideous; exostome teeth whitish yellow, narrowly triangular, 0.3–0.5 mm long, dorsal surface papillose throughout, trabeculae and median line faint; endostome whitish yellow, lightly papillose throughout, basal membranes low, segments subulate, not or narrowly perforate, not keeled, cilia rudimentary or absent. Spores rounded to irregularly oblong, 14–26 µm, smooth to lightly papillose. Calyptrae mitrate, with archegonia and/or sparse hairs, 0.5–0.8 mm long.

Illustrations. Bartram (1934, Fig. 1); Bartram (1949, Fig. 130 A–C, as *Pilotrichum amazonum*; Fig. 130 D–F, as *Pilotrichum cryphaeoides*); Crosby (1969a, Figs. 104–120, 190–192); Florschütz-de Waard (1986, Fig. 115); Sharp *et al.* (1994, Fig. 627); Churchill and Linares (1995, Fig. 43 g–i); Buck (1998, Pl. 29 7 & Pl. 32 5–10); Buck (2003, Fig. 100); Vaz (2006b, Figs. 88–98). Figure 124.

Habitat. On tree trunks, branches, twigs, vines, and rotting logs; sea level to 1400 m.

Distribution in Central America. BELIZE: Cayo: *Whitefoot 1251* (MO); Stann Creek: *Gentle 9307* (MO); Toledo: *Allen 18888* (BRM, MO). GUATEMALA. Izabal: *Steyermark 39911a* (F, FH); Petén: *Lundell 2731* (FH); Quetzaltenango: *Steyermark 33512* (F, FH); Suchitepéquez: *Steyermark 35291* (F, FH). HONDURAS. Atlántida: *Allen 17611* (MO, TEFH); Cortés: *Morton 7638d* (US). NICARAGUA. Chontales: *Standley 9098* (F); Jinotega: *Stevens 16469* (MO); Zelaya: *Stevens 6942* (MO). COSTA RICA. Cartago: *Crosby 3656* (MO); Guanacaste: *Crosby 3852A* (MO); Limón: *Steere CR-24* (NY); Puntarenas: *Liesner 2972a* (MO); San José: *Lemmon 10* (MO). PANAMA. Bocas del Toro: *Crosby 4082* (MO); Canal Area: *Nee 6907* (MO); Chiriquí: *Allen 5475* (MO); Colón: *Crosby 10768* (MO); Darién: *Williams 1051* (F, FH, NY); Panamá: *Crosby 10407* (MO), San José Island: *Erlanson 122* (FH); San Blas: *Allen 4972B* (MO); Veraguas: *Crosby 10249* (MO), Bahia Honda: *Taylor 1112* (FH), Isla de Coiba: *Mendez 67* (FH, US).

World range: Mexico; Central America; Caribbean; Western and Northern South America.

Pilotrichum evanescens is a medium-sized species with pinnately or bipinnately branched stems. It has a weakly stipitate habit, with poorly differentiated stipe leaves that are erect-spreading when wet and have recurved margins. Its leaves are erect when dry, strongly decurrent, and have relatively

short costae that diverge throughout their lengths and sometimes end in a forward-pointing tooth. Occasionally, the costae are weakly crested, with the crest one cell high and restricted to the uppermost part of the costae. The leaf cells are variable in size (10–25 μm), but regularly elliptic to oblong, and they have numerous quadrate to short-rectangular cells at the basal angles. Asexual propagula are often found in *P. evanescens*. They are uniseriate, papillose-roughened, hyaline when young but reddish brown when old, and on the dorsal side of the costae at the leaf base. Although the setae of *P. evanescens* are variable in length both within and between collections, the capsules are consistently exserted. The opercula are conic-rostrate, and the short, mitrate calyptrae bear archegonia remnants as well as sparse hairs.

The Cocos Island endemic, *Pilotrichum rugifolium*, is the only Central American species likely to be morphologically confused with *P. evanescens*. The two species have a similar aspect when dry and have leaves stiffly erect, with propagula borne dorsally at the base of the costa, a comparable areolation, and relatively short, weak costae that diverge throughout their lengths. *Pilotrichum rugifolium* has strongly rugose leaves, and this feature will usually separate it from *P. evanescens*. However, *P. evanescens* sometimes has lightly rugose leaves, and so the feature should be used with caution. *Pilotrichum rugifolium* also differs from *P. evanescens* in having larger stem leaves (1.6–2.0 mm vs. 1.0–1.6 mm long) that are narrowly oval rather than broadly ovate, and immersed capsules.

Pilotrichum fendleri is similar to *P. evanescens* in having exserted capsules, and in leaf shape as well as overall areolation. Its leaves differ from those of *P. evanescens* in being erect-incurved to catenulate when dry, and in having longer, stronger, often dorsally crested costae, elongate apical leaf cells, and dorsal propagula borne at the apex of the costae.

6. *Pilotrichum fendleri* Müll. Hal., Linnaea 42: 492. 1879. Protologue [Venezuela. *Fendler*] *Nr. 93. Pilotrichum fendleri*, sin. loc. Type. Musci Fendleriani Venezuelenses *93. Pilotrichum fendleri* n.sp. (FH, isotype).

Pilotrichum mucronatum Mitt. var. *elongatum* Renauld & Cardot, Bull. Soc. Bot. Belgique 32(1): 183. 1893 [1894]. Protologue. [Costa Rica] Forêts du Rio Naranjo, 200–250 m (*Pitt.*[*ier*] *n° 5697*). Type. Costa Rica, Forêts du Rio Naranjo, 200–250 m, leg. *Pittier & Tonduz 5697* (FH, US, isotypes).

Pilotrichum tonduzii Renauld & Cardot, Bull. Soc. Bot. Belgique 32(1): 184. 1893 [1894]. Protologue. [Costa Rica] Forêts du Río Naranjo, (*Pitt.*[*ier*] *n° 5698*).

Eupilotrichum fasciculatum Müll. Hal., Bull. Herb. Boissier 5: 204. 1897, invalid name, genus invalid, lacks a description. *Pilotrichum fasciculatum* Müll. Hal. *ex* Paris, Index Bryol. Suppl. 273. 1900. Protologue. Guatemala, sine loco speciali, quam linteum involucris serviens (Packmaterial) in Museo zoologico Florentino 1892, Hb. Levier. Type. America centralis e viciniis urbis Guatémala inde accepit Museum Zoologico Florentino. 1892, legit *indigenus* [Bryotheca E. Levier] (FH, isotype).

Pilotrichum pallidum E. B. Bartram, Contr. U.S. Natl. Herb. 26: 98. 1928. Protologue. On tree, El Arenal, Province of Guanacaste, Costa Rica, altitude 485 to 600 meters, *Paul C. Standley* and *Juvenal Valerio*, January 18 and 19, 1926, *no. 45247*. Types. Costa Rica. On tree, El Arenal, Provincia de Guanacaste, altitude 485–600 meters, *Paul C. Standley & Juvenal Valerio No. 45247* (FH, holotype; FH, US, isotypes).

Plants medium-sized to robust, 3–25 cm long, reddish yellow, yellow green, green, or pale green. Stolons creeping; rhizoids smooth, reddish brown, from clusters of initials abaxial to the leaf insertions, on stolons, and at the base of primary stems. Stems erect to pendent, regularly pinnately to bipinnately branched, evenly foliate; stems in cross section with sclerodermis of 4–8 rows of small, very thick-walled, red cells, cortical cells enlarged, firm- to thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia narrowly foliose to filamentous. Stipe leaves appressed when dry, erect when wet, oblong-triangular to triangular, 0.8–1.4 mm long; margins narrowly recurved throughout; costae strong and double, dark red across the leaf insertions. Stem and branch leaves erect-incurved or catenulate when dry, erect-spreading when wet. Stem leaves ovate to broadly ovate, 0.8–1.2 mm long, at times undulate, acute to obtuse-mucronate, decurrent; margins subentire to serrulate throughout, plane or sometimes recurved on one side at midleaf; costae strong, double, reaching 0.8–0.9 the leaf length, more or less parallel throughout, not or weakly crested, crest one cell high, toothed below, ending in a stout, forward-pointed tooth; cells smooth or prorate, oval, elliptic to oblong, 6–12 μm long, thick-walled, at times porose, subapical cells usually longer than surrounding cells; alar cells not or weakly differentiated, cells across the insertions reddish, porose. Branch leaves ovate to

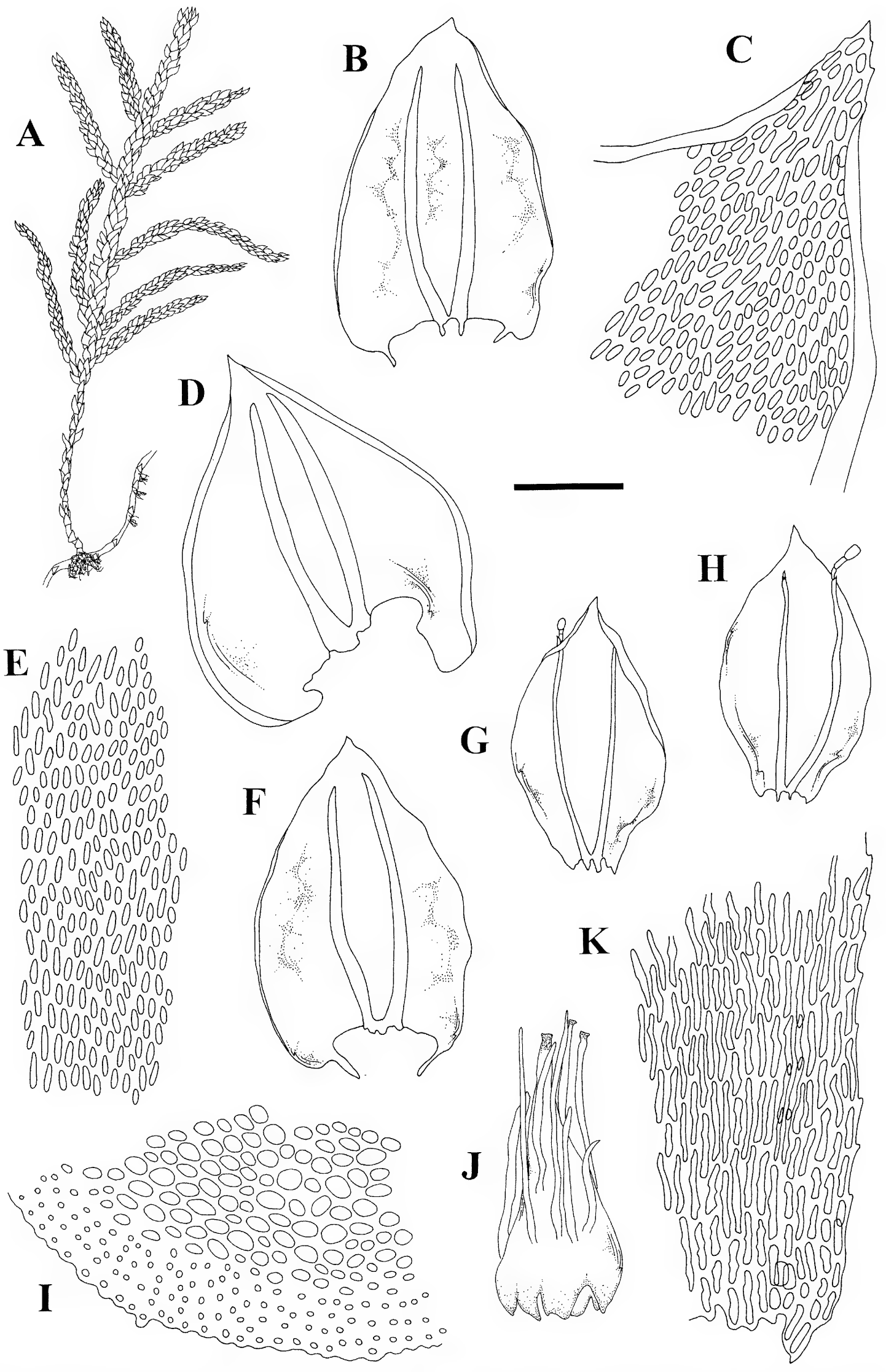


Figure 125. *Pilotrichum fendleri*. A. Habit. B & D. Stem leaves. C. Leaf apex. E. Median leaf cells between the costae. F–H. Branch leaves. I. Stem in cross section. J. Calyptra. K. Basal and alar cells. Scale in mm: bar = 0.05 (C, E, K); bar = 0.06 (I); bar = 0.28 (B, D, F–H); bar = 0.36 (J); bar = 5.0 (A). A from *Allen 18748*; B, D, F, I from *Allen 18513*; all other figure parts from *Allen 19033*.

broadly ovate, 0.6–0.9 mm long, often undulate, acute to obtuse-mucronate, decurrent; margins subentire to serrulate throughout, plane or inflexed; costae strong, double, reaching 0.8–0.9 the leaf length, more or less parallel throughout, dorsal crest 1–2 cells high, margins of crest serrulate, at times toothed below and ending in a stout, forward-pointed tooth; cells smooth or prorate, oval, elliptic to ovate, 4–11 µm long, thick-walled, at times porose, subapical cells usually longer than surrounding cells; alar cells long-rectangular, cells across the insertions reddish, porose. Asexual propagula from upper, dorsal side of the costae. Dioicous. Perichaetia on short lateral branches on stems and branches; perichaetial leaves lanceolate, 0.8–1.0 mm long. Setae short, flexuose, 1.2–2.0 mm, roughened-papillose above. Capsules exserted, erect, oblong-cylindric, symmetric, 1–2 mm long; exothecial cells dark red, oblate in 3–5 rows at mouth, those below short-rectangular, thick-walled; stomata on neck; opercula short-rostrate, 0.7–0.9 mm long; annuli rudimentary, of several rows of firm-walled, persistent cells; peristome diplolepideous; exostome teeth pale yellow, narrowly triangular, dorsal surface papillose throughout, trabeculae and median line faint; endostome yellow, lightly papillose throughout, basal membranes low, segments subulate, not or narrowly perforate, not keeled, cilia rudimentary or absent. Spores rounded to irregularly oblong, 14–20 µm, lightly papillose. Calyptrae mitrate, with archegonia and long, somewhat papillose hairs, 0.5–0.7 mm long.

Illustrations. Bartram (1928a, Fig. 30 A–F); Crosby (1969a, Figs. 96–103, 194–195); Florschütz-de Waard (1986, Fig. 117); Sharp *et al.* (1994, Fig. 625 C & D); Buck (1998, Pl. 29 12, Pl. 35 1–5); Buck (2003, Fig. 101). Figure 125.

Habitat. On tree trunks and branches, roots, vines, and logs, occasionally on rocks near or in streams; near sea level to 1800 m.

Distribution in Central America. BELIZE. Toledo: *Allen 19033* (BRH, MO). GUATEMALA. Alta Verapaz: *Steyermark 44814* (F, FH, NY, US); Izabal: *Steyermark 38905* (F, FH). HONDURAS. Copán: *Allen 17748* (MO); Olancho: *Allen 12796* (MO). NICARAGUA. Jinotega: *Stevens 16630* (MO). COSTA RICA. Alajuela: *Standley & Torres 46938* (FH, NY, US); Cartago: *Standley & Valerio 46877* (FH, NY, US); Guanacaste: *Crosby 3848* (MO); Limón: *Crosby 3687* (MO); Puntarenas: *Crosby 2687* (MO). PANAMA. Bocas del Toro: *Allen 5848* (MO); Canal Area: *Steyermark 40884* (FH, US); Chiriquí: *Cornman 3096* (F, FH, MO); Coclé: *Folsom et al. 5715A* (FH, MO, NY, PMA, US); Colón: *Crosby 10791* (MO); Panamá: *Crosby 4363* (F, MO); Veraguas: *Crosby 10243* (MO, PMA), Isla Coiba: *Seemann* (NY).

World range: Central America; Caribbean; Western and Northern South America.

Pilotrichum fendleri is one of the largest and most common *Pilotrichum* species in Central America. It often occurs pendent from tree trunks, and, unlike most other *Pilotrichum* species, is occasionally found on rocks along or in streams. Its plants are regularly pinnate to bipinnate and frequently reddish yellow. *Pilotrichum fendleri* has ovate to broadly ovate leaves that are erect-incurved or catenulate when dry. The leaves are often undulate, with subentire to minutely serrulate margins and long costae that are more or less parallel throughout their lengths. Although the costae have variably developed dorsal crests, they consistently end in a stout tooth. The leaf cells of *P. fendleri* are oval, elliptic to oblong, with the subapical cells usually longer than surrounding cells and elongate in the alar regions. Sporophytically, *P. fendleri* has short, flexuose setae and exserted capsules. Most Central American collections of *P. fendleri* have leaf propagula present at or near the tip of the costae.

Pilotrichum andersonii and *P. bipinnatum* are the Central American species most likely to be confused with *P. andersonii*. All three species are comparable in size, and they have similarly shaped leaves that are erect-incurved to catenulate when dry. Microscopically, they are similar in costal length, as well as leaf cell shape. *Pilotrichum andersonii* and *P. fendleri* also have costae with narrow dorsal crests and propagula produced near the costal apex. *Pilotrichum andersonii* differs from *P. fendleri* in having non-undulate leaves with short, homogeneous apical leaf cells. *Pilotrichum bipinnatum* is especially close to *P. fendleri*; Crosby (1969a) found some collections that could not be confidently placed in either species. Both species differ from all other Central American *Pilotrichum* species in having heterogeneous apical leaf cells. *Pilotrichum bipinnatum* differs from *P. fendleri* in having synoicous plants that never produce leaf propagula and shorter setae (1–1.7 mm vs. 1.5–2.5 mm).

7. *Pilotrichum ramosissimum* Mitt., J. Linn. Soc., Bot. 12: 388. 1869. *Callicosta ramosissima* (Mitt.) Crosby, Bryologist 81: 436. 1978. Protologue. Andes Bogotenses, in sylvis supra Pacho (6000 ped.), ad corticem arborum laevem, *Weir, n. 133.* Type. [Colombia] Pacho, *Weir, Musc. Nov. Gran. 133* (NY, holotype; FH, isotype).

Callicosta delicatula Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 227. 1872. *Pilotrichum delicatulum* (Besch.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 236. 1877. *Pilotrichella delicatula* (Besch.) Schimp. *ex* Paris, Index Bryol. 943. 1897. Protologue. [Mexico] Oajaca, 4–5000 ped. alt. (*Galeotti n^{o} 6882* in herb. Mus. par.); Huatusco (*Liebmann* in herb. Schimper).

Eupilotrichum filigranum Müll. Hal., Bull. Herb. Boissier 5: 204. 1897, invalid name, genus invalid, lacks a description. *Pilotrichum filigranum* Müll. Hal. *ex* Paris, Index Bryol. Suppl. 273. 1900. Protologue. [Guatemala] Coban, 4400 ped. altum, Octobri 1888: *v. Türckheim* in Hb. Brotheri.

Plants slender and wiry, 4–7 cm long, yellow green to reddish yellow or reddish brown. Stolons creeping; leaves appressed to spreading, oblong-triangular, 0.4–0.6 mm long, costae strong and double, dark red across the leaf insertions; rhizoids smooth to lightly roughened, reddish brown, from clusters of initials abaxial to the leaf insertions, on stolons, and at the base of primary stems. Stems erect to pendent, regularly bipinnately branched, branches determinate or indeterminate, evenly foliate; stems in cross section with sclerodermis of 3–6 rows of small, very thick-walled, red cells, cortical cells enlarged, thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia narrowly foliose to filamentous. Stem and indeterminate primary branch leaves erect to erect-appressed when dry, erect-spreading when wet, ovate to broadly ovate, 0.6–1.4 mm long, acute to broadly acute, decurrent; margins subentire to serrate above, plane or narrowly recurved below; costae strong, double, reaching 0.8–0.9 the leaf length, often narrowly crested, ending in a large, forward-pointing tooth; cells smooth to obscurely prorate, elliptic to narrowly elliptic, 8–22 µm long, at times linear (to 35 µm), thick-walled, occasionally porose; alar cells not or weakly differentiated, cells across the insertions elongate, often reddish, porose. Determinate branch leaves ovate to broadly ovate, acute to narrowly acute, 0.5–0.8 mm long, narrowly decurrent; margins subentire to serrulate, plane; costae strong, double, reaching 0.8 the leaf length, at times narrowly crested, toothed at tips; cells smooth or prorate, oblong to elliptic, 3–25 µm long, thick-walled, occasionally porose; alar cells not or weakly differentiated, cells across the insertions reddish, porose. Asexual propagula occasionally present on upper, dorsal surface of the costae. Dioicous. Perichaetia and perigonia on short lateral branches on stems and branches. Setae short, flexuose, 1–2 mm, smooth to somewhat roughened above. Capsules exserted, erect, oblong-cylindric, symmetric, 1.0–1.5 mm long; exothecial cells dark red, oblate in 3–5 rows at mouth, those below short-rectangular, thick-walled; stomata on neck; opercula conic-rostrate, 0.5–1.0 mm long; annuli of several rows of enlarged, deciduous cells; peristome diplolepideous; exostome teeth pale yellow, narrowly triangular, 0.8 mm long, dorsal surface papillose throughout, trabeculae and median line faint; endostome yellow, lightly papillose throughout, basal membranes low, segments subulate, not or narrowly perforate, not keeled, cilia absent or rudimentary. Spores variable in size within single capsules, rounded to irregularly oblong, 14–28 µm, lightly papillose. Calyptrae conic-mitrate, irregularly lobed, with numerous hairs and remnant archegonia, 0.5 mm long.

Illustrations. Bartram (1949, Fig. 131 A–C); Crosby (1969a, Figs. 76–81, 180); Sharp *et al.* (1994, Fig. 625 a & b). Figure 126.

Habitat. On tree trunks (sometimes festooning), branches, roots, shrubs, vines, logs, and occasionally on rocks along streams; 70–1840 m.

Distribution in Central America. BELIZE. Toledo: *Allen 18748B* (MO). GUATEMALA. Alta Verapaz: *Standley 71701a* (F, FH). HONDURAS. Comayagua: *Allen 13949* (MO); Cortés: *Morton 7638b* (US); Olancho: *Allen 12777A* (MO). COSTA RICA. Alajuela: *Brenes 19147* (F, FH, NY); Cartago: *Standley & Torres 50889* (FH, NY, US); Guanacaste: *Crosby 3844C* (MO); Heredia: *Standley & Valerio 50047* (FH, NY, US); Limón: *Standley 36886* (NY); Puntarenas: *Lyons 314* (MO); San José: *Crosby 10879* (MO). PANAMA. Bocas del Toro: *Allen* 5686 (MO); Canal Area: *Steyermark & Allen 17163* (MO); Chiriquí: *Cornman 3120* (F, FH, MO, US); Coclé: *McPherson 12437C* (MO); Darién: *Allen 8935* (MO); Panamá: *Crosby 10424* (MO); Veraguas: *Crosby 10912* (FH, MO).

World range: Mexico; Central America; Western and Northern South America.

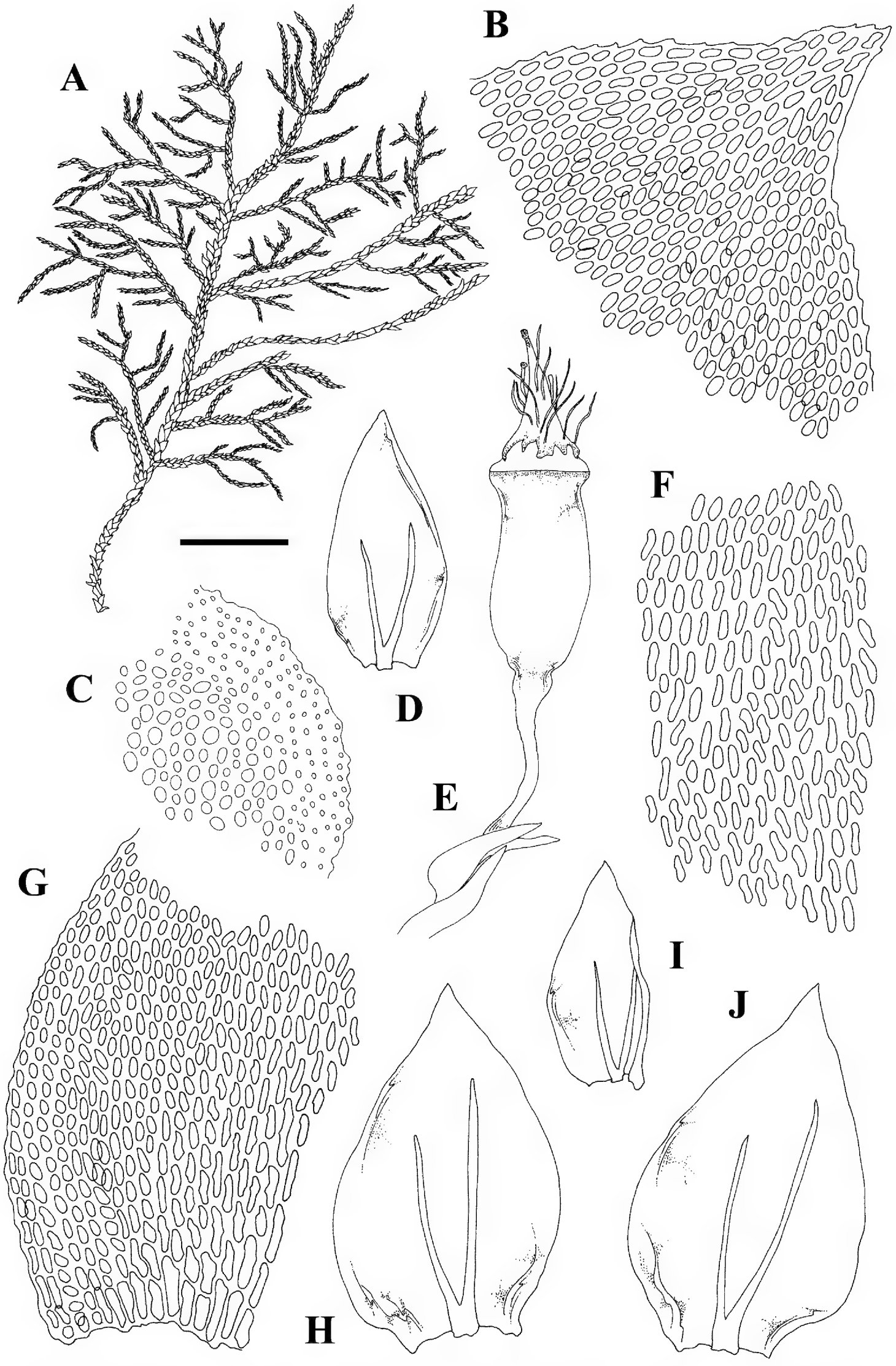
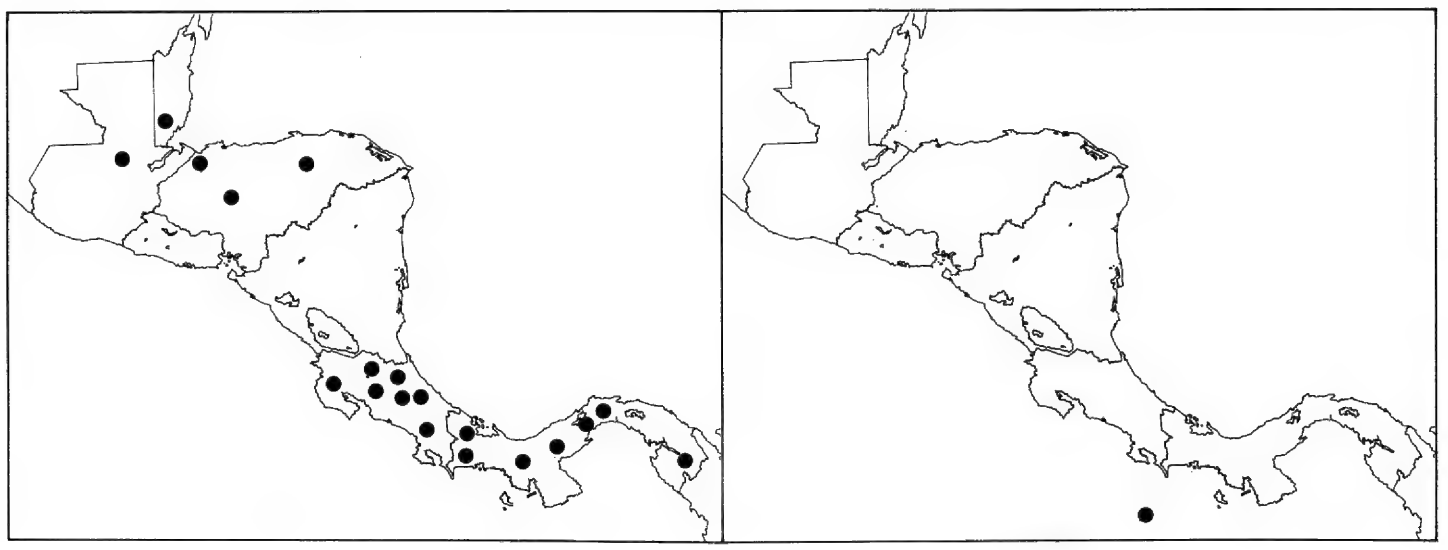


Figure 126. *Pilotrichum ramosissimum*. A. Habit. B. Leaf apex. C. Stem in cross section. D & I. Branch leaves. E. Seta, capsule, and calyptra. F. Median leaf cells between the costae. G. Basal and alar cells. H & J. Stem leaves. Scale in mm: bar = 0.05 (B, F, G); bar = 0.08 (C); bar = 0.2 (D, H–J); bar = 0.9 (E); bar = 5.0 (A). A from *Crosby & Crosby 6389*; E from *Allen 5652*; all other figure parts from *Allen 5590*.



Pilotrichum ramosissimum *Pilotrichum rugifolium*

Pilotrichum ramosissimum is a slender, often wiry species with regularly bipinnate stems. Its ultimate branches are filiform and have imbricate leaves. The most distinctive feature of the species is the presence of indeterminate primary branches that are produced at regular intervals and give the plants a stair-step appearance somewhat similar to that of *Hylocomium splendens*. *Pilotrichum ramosissimum* has ovate to broadly ovate stem and branch leaves that are erect to erect-appressed when dry and have acute to broadly acute apices. Its leaves have serrate margins that are usually plane, long costae with narrow dorsal crests, and strongly toothed apices. The leaf cells are smooth to obscurely papillose, elliptic to narrowly elliptic, and vary greatly in length. The sporophytes of *P. ramosissimum* have short, flexuose setae, conic-rostrate opercula, and exserted capsules. *Pilotrichum ramosissimum* collections only rarely have propagula present on the upper parts of the costae.

Pilotrichum asperifolium is the only other Central American species of *Pilotrichum* with indeterminate branches, but, unlike the indeterminate branches of *P. ramosissimum*, they are only occasionally branched and do not significantly contribute to the vertical growth to the plants. In addition, *P. asperifolium* differs from *P. ramosissimum* in its more robust size and in often having propagula along the leaf margins as well as on the upper parts of the costae. When the marginal leaf propagula in *P. asperifolium* detach, they leave behind distinctive notches in the margins. This is especially evident in older leaves that lack propagula but have deeply notched margins.

8. *Pilotrichum rugifolium* Müll. Hal., Syn. Musc. Frond. 2: 177. 1851. Protologue. Insula Owyhee Australiae: Hook. Hb [*Menzies*]. Type. *N. hypnoides*. Owyhee 1794. *A. Menzies No. 96* (BM, isotype).

Plants medium-sized to large, 6–10 cm long, green, yellow green, or reddish yellow. Stolons creeping; rhizoids smooth to lightly roughened, reddish brown, from clusters of initials abaxial to the leaf insertions, on stolons, at base of primary stems, and stems and branches when they contact the substrate. Stems erect to pendent, bipinnately branched; branches determinate, evenly foliate; stems in cross section with sclerodermis of 4–7 rows of small, very thick-walled, red cells, cortical cells enlarged, thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia narrowly foliose to filamentous. Stipe leaves closely spaced, erect to erect-spreading when wet, ovate, 1.4–2.0 mm long, long-decurrent; margins narrowly recurved; costae strong and double, 0.7–0.8 the leaf length, dark red across the leaf insertions, diverging above, tips at times projecting as spines and weakly crested. Stem and primary branch leaves erect-flexuose when dry, erect-spreading when wet, conspicuously rugose. Stem leaves narrowly oval, 1.6–2.0 mm long, acute to broadly acute, decurrent; margins serrulate and plane above, subentire and narrowly recurved below; costae strong, double, diverging throughout, reaching 0.6–0.8 the leaf length, at times weakly crested, crest 1–2 cells high, toothed at apex and with a few low teeth on the upper 1/3; upper cells strongly papillose to nearly smooth, elliptic to oblong, 10–20 µm long, thick-walled, occasionally porose, marginal cells similar to the interior cells;

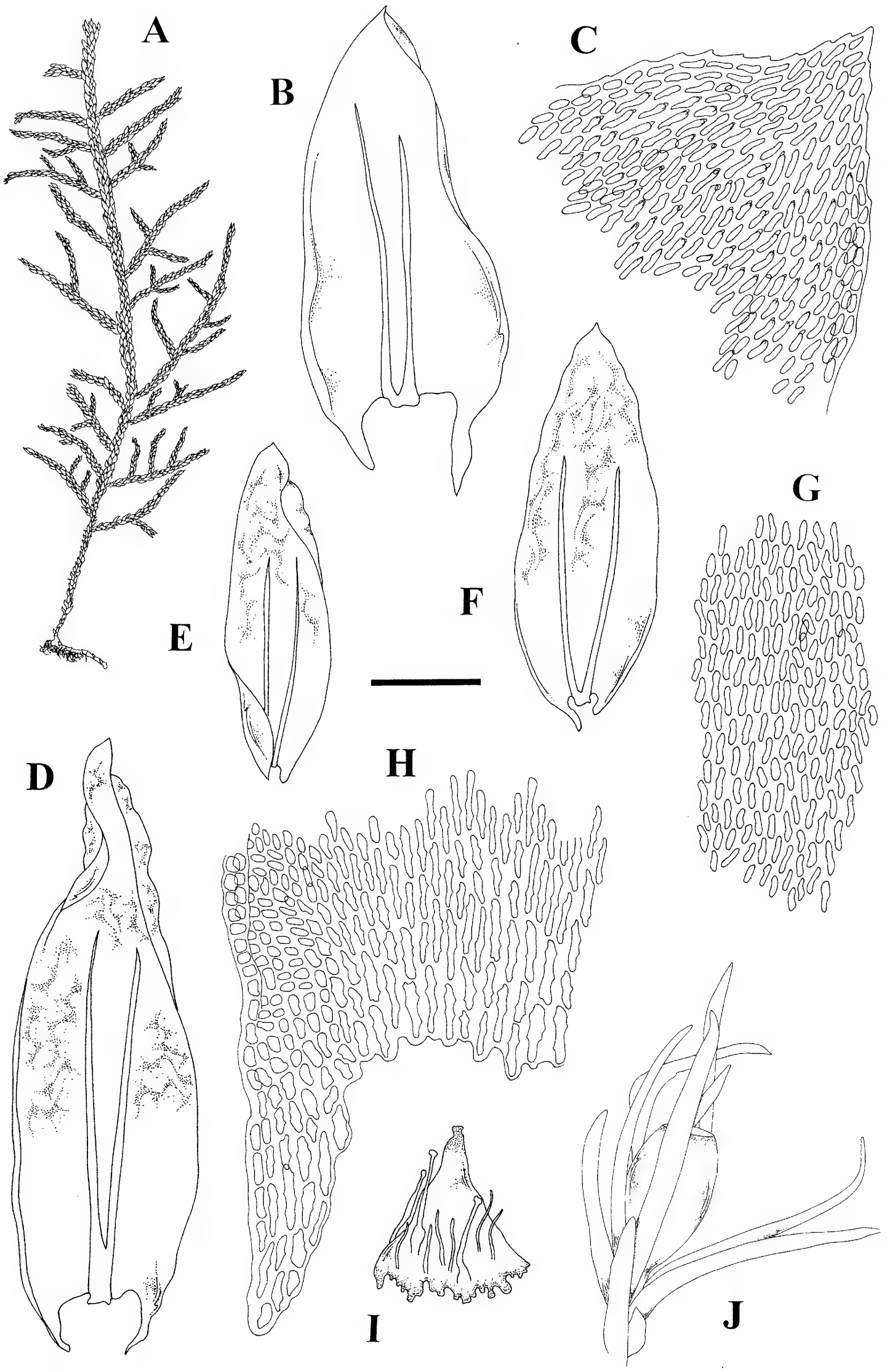


Figure 127. *Pilotrichum rugifolium*. A. Habit. B. Stipe leaf. C. Leaf apex. D. Stem leaf. E & F. Branch leaves. G. Median cells between the costae. H. Basal and alar cells. I. Calyptra. J. Capsule. Scale in mm: bar = 0.06 (C, G, H); bar = 0.5 (B, D–F, I); bar = 0.8 (J); bar = 10.9 (A). A from *Dressler*; B from *Valerio 1094*; D from *Klawe s.n.*; I, J from *Gómez 17992*; all other figure parts from *Gómez 18018*.

basal cells elongate, porose; alar cells not or weakly differentiated as irregularly triangular, porose cells. Primary branch leaves elliptic to ovate, rounded-acute to obtuse, apices often galeate, 1.2–1.5 mm long, decurrent; margins serrulate above, serrulate to subentire below, plane above, reflexed below; costae strong, double, reaching 0.6–0.8 the leaf length, at times crested, crest one cell high and toothed along upper margin, ending in a forward-pointing spine; upper cells papillose to smooth, narrowly elliptic to narrowly oblong, 10–25 µm long, thick-walled, occasionally porose; basal cells elongate, porose; alar cells not or weakly differentiated as a few rectangular cells. Asexual propagula on dorsal surface at base of costae. Dioicous. Perichaetia and perigonia on short lateral branches on stems and branches. Setae short, 0.6 mm long, thickened at base, smooth, yellow when young, red when mature. Capsules immersed, erect, oblong to oblong-cylindric, symmetric, 1.0–1.5 mm long; exothecial cells dark red, oblate in 3–5 rows at mouth, those below subquadrate to short-rectangular, firm-walled; stomata immersed on neck; opercula conic-rostrate, 0.5–0.8 mm long; annuli of several rows of enlarged, deciduous cells; peristome diplolepideous; exostome teeth whitish yellow, narrowly triangular, 0.3–0.5 mm long, dorsal surface papillose throughout, trabeculae and median line faint; endostome whitish yellow, lightly papillose throughout, basal membranes low, segments subulate, not or narrowly perforate, not keeled, cilia rudimentary. Spores rounded to irregularly oblong, 22–36 µm, smooth to lightly papillose. Calyptrae mitrate, with archegonia and/or sparse hairs, 0.5–0.8 mm long.

Illustrations. Bartram (1933b, Fig. 3); Crosby (1969a, Figs. 155–162, 181). Figure 127.
Habitat. On tree trunks and branches; 20–232 m.
Distribution in Central America. COSTA RICA. Cocos Island: *Weber B-14320* (FH, MO, NY, US).
World range: Endemic to Cocos Island.

Pilotrichum rugifolium is a medium-sized to large species with long stems, well-spaced branches, and long, narrowly ovate, strongly rugose stem and branch leaves. It has a weakly stipitate habit, with weakly differentiated stipe leaves that are erect-spreading when wet and have recurved margins. Its stem and branch leaves are decurrent and have relatively short costae that diverge throughout their lengths and sometimes end in a forward-pointing tooth. The costae are sometimes weakly crested, with the crest 1–2 cells high and restricted to the uppermost part of the costa. The leaf cells are regular in form, elliptic to oblong, and fairly long (10–25 µm). When present, the asexual propagula of *P. rugifolium* occur on the dorsal side of the costae at the leaf base. The sporophytes of *P. rugifolium* have very short setae that are curiously thickened at base, conic-rostrate opercula, and immersed capsules.

Pilotrichum corrugatum and *P. evanescens* are the only Central American species likely to be confused with *P. rugifolium*. *Pilotrichum corrugatum*, like *P. rugifolium*, is endemic to Cocos Island, and these species are similar in overall aspect, leaf shape, and in having strongly rugose leaves. Although the species can be more or less similar in size, *Pilotrichum rugifolium* is often more robust than *P. corrugatum*, which has well-differentiated stipe leaves that are squarrose above when wet. In addition, the leaves of *P. corrugatum* are bordered by elongate to sigmoid cells and they have longer costae that are more or less parallel throughout their lengths. Finally, *P. corrugatum* has exserted capsules and propagula that occur at the apex of the costae; in contrast, *P. rugifolium* has immersed capsules and propagula at the base of the costae.

Pilotrichum evanescens is similar to *P. rugifolium* in having short, diverging costae and basal propagula. Although *P. evanescens* is a widely distributed species found throughout the Caribbean and Central America as well as parts of South America, it does not occur on Cocos Island. Furthermore, its leaves are plane or sometimes slightly rugose, it has longer setae (0.6–1.4 mm), and the capsules are exserted.

The type of *Pilotrichum rugifolium* was collected by Archibald Menzies during the Vancouver expedition to the Pacific Northwest. Its odd type locality has sometimes been considered a "phonetic spelling of Hawaii" (Bartram 1933a, 1933b). Bartram (1933a), however, excluded the species from Hawaii because it was otherwise unknown there, and he considered *Pilotrichum* nearly restricted to the American tropics. John Thomas Howell (*in* Bartram 1933b) found that the Vancouver expedition stopped at Cocos Island from 23–27 January 1795. From this information Bartram (1933b) concluded "the collection was incorrectly labeled and that *P. rugifolium* is endemic to Cocos Island."

DALTONIACEAE

Daltoniaceae Schimp., Syn. Musc. Eur. 478. 1860.

Daltoniaceae H. A. Mill., Phytologia 21: 250. 1971, superfluous name.
Distichophyllaceae H. A. Mill., Phytologia 21: 249. 1971.
Adelotheciaceae W. R. Buck, Brittonia 39: 214. 1987.

Plants simple or sparingly branched, erect, prostrate, or pendent. Stems usually dark red; central strand absent or occasionally present; axillary hairs (2–)3–12 cells long, hyaline or with only the basal cells pigmented (sometimes several cells pigmented in *Bryobrothera*); paraphyllia absent; pseudoparaphyllia absent (filamentous to subfoliose in *Adelothecium*); rhizoids 1–3-pinnately branched, in clusters abaxial to the leaf insertions, scattered over the stem, or around branch buds. Leaves monomorphic or dimorphic with lateral leaves larger than the ventral and dorsal leaves; margins often with a border of narrow, elongate cells; costae present, single or double, variable in length (costa sometimes absent in *Distichophyllidium*); cells rounded, hexagonal, rhombic or elongate-rhomboidal, smooth. Asexual reproduction often by gemmae on main stems, reduced branches, or rhizoids. Dioicous, autoicous, or synoicous. Perichaetia and perigonia on short lateral branches. Setae short or long. Capsules erect or inclined; exothecial cells at times strongly collenchymatous; opercula rostrate; peristome diplolepideous; exostome teeth 16, dorsal (outer) plates thick and cross-striate or thin and papillose, median furrow absent or strongly developed; endostome papillose, basal membranes high or low, segments broad or linear, variously keeled, not or weakly perforate, cilia rudimentary or absent. Calyptrae mitrate, naked or hairy, usually fimbriate-fringed with unicellular or multicellular hairs.

There has been considerable controversy over the composition of the Daltoniaceae, due mostly to the presence of a large number of generic pairs that have very similar gametophytes but radically different sporophytes. Crosby (1974b) restricted the family to those genera having a daltoniaceous peristome: exostome teeth papillose, with ventral plates narrower than the dorsal plates and median furrow absent; endostome papillose, with low basal membranes and cilia absent. Buck (1987, 1988), taking the opposite approach, stressed gametophytic similarities and placed in the Daltoniaceae only members of the Hookeriales that lacked pseudoparaphyllia and that had leaf costae typically single, leaves usually bordered, and calyptrae mitrate and fringed at the base.

Whittemore and Allen (1989) also re-evaluated the Daltoniaceae/Hookeriaceae problem from a gametophytic perspective. They noted that the different peristome morphologies within the Hookeriales were correlated with important functional differences: hookeriaceous peristome xerocastique, *i.e.*, reflexed when dry and incurved when wet; daltoniaceous peristome hygrocastique, *i.e.*, incurved when dry and outcurved when wet. Furthermore, they observed that the various daltoniaceous peristomes were not uniform in morphology and that similar morphologies occurred in other pleurocarpous mosses. Finally, because of the lack of correlation in the Hookeriales between characters of the peristome and other organs, they concluded the daltoniaceous peristome had arisen more than once in the order. They defined the Daltoniaceae as a group of mosses with usually unicostate leaves, rhizoids branched (sometimes densely) and scattered over the cortex, axillary hairs (2–)3–10 cells long, plants usually unbranched, stem cortex deeply red pigmented, and mitrate, fringed calyptrae. Buck *et al.* (2005) examined the Hookeriales using molecular and morphological techniques. Although the list of genera they placed in the Daltoniaceae included some not considered by Whittemore and Allen (1989), the composition of the Daltoniaceae in both studies was essentially the same.

1. Costae short and double; leaves serrate; setae spinose. . . . . 2. *Calyptrochaeta*
1. Costae long, ending above midleaf, single; leaves entire, serrulate, or denticulate-crenulate; setae smooth or roughened papillose 2

2. Leaves unbordered; stem epidermis thick-walled; pseudoparaphyllia filamentous; calyptrae not fringed, densely hairy; exostome teeth on dorsal surface cross-striate below . . . . . 1. *Adelothecium*
2. Leaves bordered; stem epidermis thin-walled; pseudoparaphyllia absent; calyptrae fringed, usually naked; exostome teeth papillose throughout 3

3. Leaves isophyllous, spirally arranged, variously lanceolate, carinate at base; leaf border broadened below . . . . . 3. *Daltonia*
3. Lateral and dorsal leaves differentiated, complanate, orbicular, oval, oblong, or spathulate, plane at base; leaf border uniform throughout . . . . . 4. *Leskeodon*

1. *Adelothecium* Mitt., J. Linn. Soc., Bot. 12: 391. 1869. *Distichophyllum* Dozy & Molk. sect. *Adelothecium* (Mitt.) Müll. Hal., Hedwigia 39: 269. 1900.

Plants medium-sized to robust, light green, yellowish red, golden, or brown. Stems procumbent below, pendent or projecting horizontally above, sparsely and irregularly branched, complanate-foliate; stems in cross section with thick-walled sclerodermis, enlarged, firm-walled cortex, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous to subfoliose; axillary hairs 5–12 cells long, upper cells short and bulging, all cells hyaline; rhizoids dense, from scattered initials on stems and around branch primordia, pinnately branched. Leaves dimorphic: lateral leaves wide-spreading, asymmetric, broadly ovate to obovate, ventral leaves erect, symmetric, ovate to obovate, mucronate to cuspidate, decurrent; margins plane, denticulate-crenulate throughout; costae single, strong, usually dark red, percurrent or ending in the acumen, sometimes spurred, cells above the costal tip elongate; cells in oblique rows from the costae, smooth, upper and median cells isodiametric, oval, oblong, or short-rectangular; basal cells elongate, both thick-walled, collenchymatous, porose; alar cells short rounded-rectangular to quadrate. Stems and branches often ending in slender, tapering, microphyllous points with gemmaphore-bearing branches in leaf axils, propagula fusiform, ellipsoid, or cylindrical, sometimes stalked, paired or single, uniseriate, 2–5 cells long. Dioicous. Perichaetia and perigonia on short lateral branches on stems. Setae short, flexuose, smooth to somewhat roughened. Capsules exserted, erect, ovoid to oblong, symmetric; exothecial cells rounded to subquadrate, somewhat collenchymatous; stomata present; opercula conic-rostrate; annuli rudimentary; peristome diplolepideous; exostome teeth reddish yellow, narrowly triangular, dorsal surface densely cross-striate below, papillose above, not or variably furrowed, trabeculae and median line faint; endostome yellow, lightly papillose, basal membranes high, segments keeled and perforate, cilia rudimentary or absent. Calyptrae mitrate, densely hairy.

Adelothecium is a monospecific genus found in the American tropics and East Africa (Tanzania and Madagascar). This unusual distribution pattern is also seen in *Calyptothecium* (Reese 1985), *Campylopus* (Frahm 1982), *Diphyscium* (Allen 1996), *Levierella* (Delgadillo & Buck 1988), *Phyllogonium* (Lin 1983), *Syrrhopodon* (Reese & Orbán 1986), *Trachyphyllum* (Buck & Griffin 1984), and *Tristichium* (Magill 1981).

In aspect *Adelothecium* is remarkably distinct and can be recognized in the field because it often grows on twigs and vines as dense, horizontally projecting mats. The plants are usually reddish yellow and have complanate-flattened leaves that are little changed when dry. The stems and branches are dark red, with a very thick sclerodermis, no central strand, and branch and stem buds surrounded by filamentous to subfoliose pseudoparaphyllia. Other distinctive features of its stems include intricately pinnately branched rhizoids that arise from scattered initials or around branch primordia and long, entirely hyaline axillary hairs that have short, bulging upper cells. The leaves of *Adelothecium* are dimorphic; they have strong single costae and remarkably thick-walled, collenchymatous and porose leaf cells. Plants of *Adelothecium* often have abundant propagula that are produced on specialized axillary branches.

The sporophytes of *Adelothecium* have short setae, erect, ovoid to oblong, symmetric capsules, thick-walled, collenchymatous exothecial cells, and short-rostrate opercula. *Adelothecium* has a diplolepideous peristome, with reddish brown exostome teeth that are densely cross-striate on the dorsal surface. They have a well-developed endostome, with a high basal membrane, keeled, widely perforate segments, and rudimentary cilia. The calyptrae are mitrate and densely hairy.

Adelothecium has been treated in its own family (Buck 1987, 1988, 1998), distinguished chiefly by the combination of single costae, short leaf cells, short setae, the production of propagula on reduced axillary branches, and the many-celled, hyaline axillary hairs. Buck placed the Adelotheciaceae near the Daltoniaceae. Miller (1971) put the genus in the Distichophyllaceae mainly because of its asymmetrical, complanate leaves, single costae, and unstated characters of the peristome. He also

considered the family to be closest to the Daltoniaceae. Crosby (1974b) placed *Adelothecium* in the Hookeriaceae because its peristome has cross-striate exostome teeth.

Whittemore and Allen (1989) reviewed the morphology and systematic position of *Adelothecium*. They placed the genus in the Daltoniaceae on the basis of the following features: (1) intricately pinnately branched rhizoids; (2) dark red, opaque stems; (3) strong single costae; and (4) axillary hairs that are more than four cells long and hyaline throughout. They noted *Adelothecium* differed from other members of the Daltoniaceae in several unique character states: (1) presence of filamentous pseudoparaphyllia (this feature also occurs in the newly discovered *Benitotania*); (2) rhizoid initials present around branch primordia and scattered on the stems; (3) propagula on reduced axillary branches; and (4) exostome teeth cross-striate on dorsal surface, but lacking a median furrow. Within the Daltoniaceae, Whittemore and Allen considered *Adelothecium* closest to *Crosbya*, the strongly costate species of *Distichophyllum*, and *Bryobrothera*. Recent molecular analyses (Akiyama *et al.* 2003; Buck *et al.* 2005) show *Adelothecium* to be closely related to *Bryobrothera* and *Benitotania*. These authors also place *Adelothecium* within a broadly conceived Daltoniaceae.

The name *Adelothecium* combines the Greek *adelos* (unseen, unknown, obscure) with *thekion* (a little vessel), apparently in reference to the small size of its capsules and the fact that the sporophytes arise from the underside of the stems.

Adelothecium bogotense (Hampe) Mitt., J. Linn. Soc., Bot. 12: 391. 1869. *Hookeria bogotensis* Hampe, Ann. Sci. Nat., Bot. sér. 5, 5: 303. 1866. *Mniadelphus bogotensis* (Hampe) Kindb., Enum. Bryin. Exot. Suppl. 2: 101. 1891. *Pterygophyllum bogotense* (Hampe) Paris, Index Bryol. Suppl. 288. 1900. Protologue. [Colombia] Bogotá, Azerradero, 2500 m, in sylvis editioribus, ad truncos arbor. leg. *A. Lindig*.

Mniadelphus geheebii Hampe *in* A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1877–78: 509. 1879, invalid name, lacks a description.

Distichophyllum geheebii Müll. Hal., Hedwigia 39: 269. 1900. Protologue. Brasilia, São Paulo, Apiahy, Junio 1878: *J. Puiggari* sat copiose legit; Rio de Janeiro, Serra dos Orgâos, ad truncos arborum, Decembri 1894: *E. Ule, Coll. No. 2071*; Serra Itatiaia, arboricolum: idem [*E. Ule*] Febr. 1894, *Coll. No. 2074*.

Plants medium-sized to robust, 2–10 cm long, light green, yellowish red, golden, or brown. Stems procumbent below, pendent or projecting horizontally above, sparsely and irregularly branched, complanate-foliate; stems in cross section with sclerodermis of 3–6 rows of small, very thick-walled, red cells, cortical cells enlarged, firm- to thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous to subfoliose; axillary hairs 5–12 cells long, basal 1–2 short-rectangular, upper cells short and bulging, all cells hyaline; rhizoids densely felting underside of stems, smooth, reddish brown, from scattered initials on stems and around branch primordia, intricately pinnately branched. Leaves dimorphic: lateral leaves wide-spreading, asymmetric, broadly ovate to obovate, 2.5–3.5 mm long, ventral leaves erect, symmetric, ovate to obovate, 1.5–3.0 mm long, mucronate to cuspidate, decurrent; margins plane, denticulate-crenulate throughout; costae single, strong, usually dark red, percurrent or ending in the acumen, sometimes spurred, cells above the costal tip elongate, in cross section cells very thick-walled, those in guide positions somewhat enlarged; cells in oblique rows from the costae, smooth, rarely papillose, upper and median cells isodiametric, oval, oblong, or short-rectangular, 10–22 µm long, strongly thick-walled, collenchymatous, porose; basal cells elongate, 30–90 µm, thick-walled, very porose; alar cells short rounded-rectangular to quadrate, reddish brown, porose, cells across the insertions reddish, porose. Stems and branches often ending in slender, tapering, microphyllous points with gemmaphore-bearing branches in leaf axils; propagula fusiform, ellipsoid, or cylindrical, sometimes stalked, usually paired, sometimes single, uniseriate, 2–5 cells long, 40–70 µm long. Dioicous. Perichaetia and perigonia on short lateral branches on stems; perichaetia to 2 mm long; leaves lanceolate, paraphyses not seen; perigonia to 1 mm long, leaves ovate-lanceolate; vaginulae densely hairy. Setae short, flexuose, 1.5–2.0 mm, smooth or somewhat roughened. Capsules exserted, erect, ovoid to oblong, at times constricted at the neck, symmetric, 1–2 mm long; exothecial cells rounded to subquadrate, somewhat collenchymatous; stomata immersed on neck; opercula conic-rostrate, 0.5–0.7 mm long; annuli rudimentary; peristome diplolepideous; exostome teeth reddish yellow, narrowly triangular, dorsal surface densely cross-striate

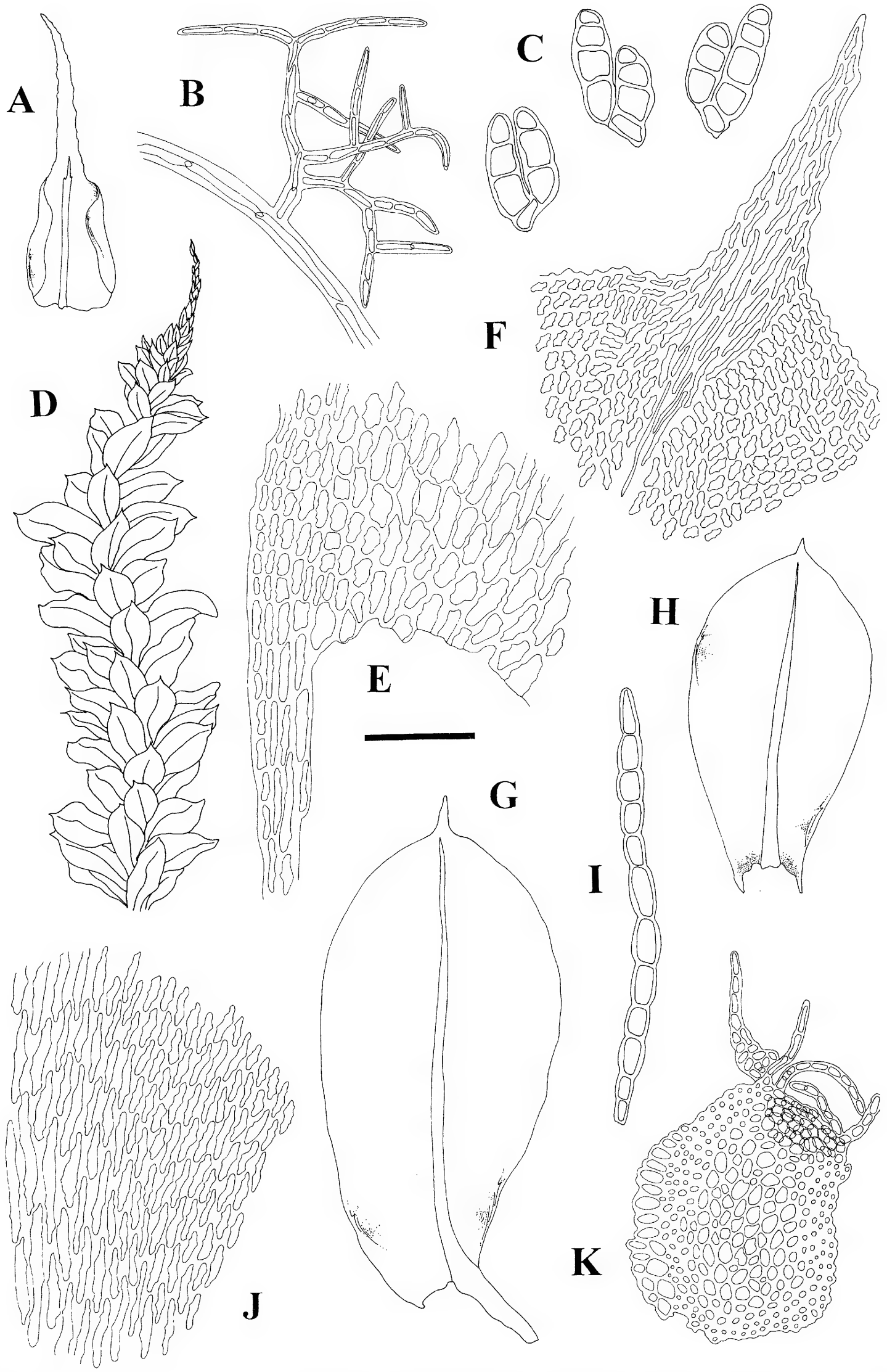
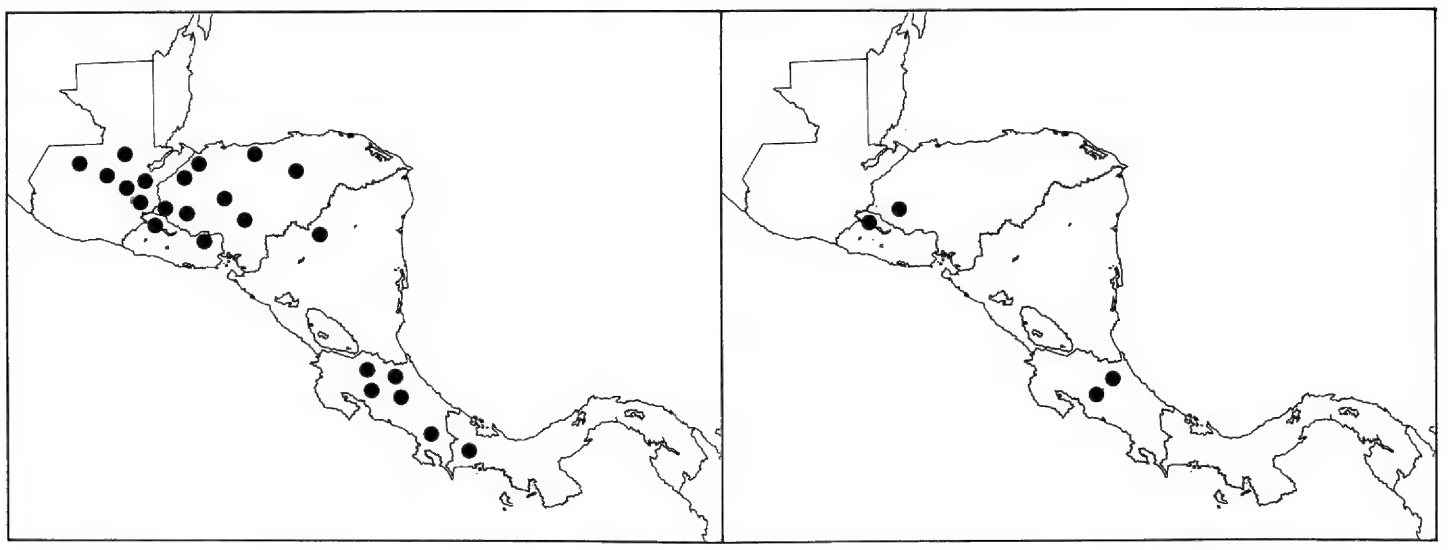


Figure 128. *Adelothecium bogotense*. A. Perichaetial leaf. B. Primary and secondary rhizoids. C. Gemmae. D. Habit. E. Basal and alar cells. F. Leaf apex. G. Ventral leaf. H. Lateral leaf. I. Axillary hair. J. Median leaf cells near costa. K. Stem in cross section with pseudoparaphyllia. Scale in mm: bar = 0.06 (B, C, I); bar = 0.08 (E, F, J); bar = 0.13 (K); bar = 0.6 (A); bar = 0.9 (G, H); bar = 3.2 (D). B, K from *Crosby & Crosby 5841*; all other figure parts from *Allen 12358.*



Adelothecium bogotense *Calyptrochaeta haitensis*

below, papillose above, not or variably furrowed, trabeculae and median line faint; endostome yellow, lightly papillose, basal membranes high, segments keeled and perforate, cilia rudimentary or absent. Spores rounded, 11–15 µm, lightly papillose. Calyptrae mitrate, densely hairy, 1 mm long.

Illustrations. Brotherus (1907a, Fig. 924 A–E); Brotherus (1925, Fig. 598 A–E); Bartram (1949, Fig. 132 G–I); Welch (1966, Figs. 1–24); Ochyra *et al.* (1992, Figs. 1–26); Sharp *et al.* (1994, Fig. 580); Churchill and Linares (1995, Fig. 1 a–f); Duarte Bello (1997, Pl. 236); Buck (1998, Pl. 6); Gradstein *et al.* (2001, Fig. 81 A–G). Figure 128.

Habitat. On tree trunks, branches, twigs, and vines, occasionally on humus in cloud forests; 1360–2600 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: *Standley 89996* (F, FH); Baja Verapaz: *Sharp 5171* (NY); El Progreso: *Sharp 2742* (FH, NY, US); Jalapa: *Steyermark 32769a* (F, FH); Quiché: *Sharp 2519* (FH, NY); Zacapa: *Steyermark 43228* (F, FH, MO, NY). EL SALVADOR. Morazán: *Winkler 586* (TUB); Santa Ana: *Winkler 582* (TUB). HONDURAS. Atlántida: *Allen 17522* (MO, TEFH); Comayagua: *Allen 13764* (MO); Cortés: *Allen 14175* (MO); Francisco Morazán: *Allen 12358* (MO); Lempira: *Allen 12215* (MO); Ocotepeque: *Allen 14470* (MO); Olancho: *Allen 12677* (MO); Santa Bárbara: *Allen 11681* (MO). NICARAGUA. Jinotega: *Crosby 2728* (DUKE). COSTA RICA. Alajuela: *Standley 47829a* (FH); Cartago: *Crosby & Crosby 5845* (MO); Heredia: *Crosby 9701* (MO); Puntarenas: *Crosby 9945* (MO); San José: *Standley & Valerio 48259* (NY, US). PANAMA. Chiriquí: *Cornman 3138* (F, FH).

World range: Mexico; Central America; Caribbean; Western and Northern South America, Brazil; East Tropical Africa, Western Indian Ocean.

Adelothecium bogotense is an epiphyte nearly confined in Central America to cloud forests. The plants often grow on twigs and vines as flattened mats that project horizontally. In the field the species is frequently yellowish red, and its leaves have a strong single costa that, especially in the lower ones, is dark red. The stems and main branches typically taper to microphyllous tips, which bear numerous, naked secondary branches that have abundant (usually paired) propagula. Stems of *A. bogotense* have filamentous pseudoparaphyllia and dense, felting, pinnately branched, reddish brown rhizoids that arise from initials scattered on the stem or around branch primordia. It is a medium-sized to robust species with flattened, dimorphic leaves that are scarcely altered when dry. The lateral leaves are mostly obovate and asymmetric, while the ventral leaves are smaller, typically ovate, and symmetric. Both leaf types are mucronate to cuspidate with percurrent or subpercurrent costae and plane, denticulate-crenulate leaf margins. The length of the costae in this species seems to be age-determinate since leaves with subpercurrent costae are usually found on the lower parts of the stems and branches. The leaf cells typically radiate in oblique rows from the costa and have thick, collenchymatous walls. Although Brotherus (1907a, 1925) figured the leaf cells as stoutly papillose, they

are usually smooth. The upper cells are short, the basal cells elongate, and the alar cells, although differentiated, are not especially well developed. Sporophytically, *A. bogotense* has short setae and exserted, erect, symmetric capsules. Its peristome has exostome teeth densely cross-striate on the dorsal surface and the endostome, although well developed, has rudimentary cilia. The calyptrae are mitrate and densely hairy.

Within Central American Daltoniaceae only *Calyptrochaeta haitensis* is comparable to *Adelothecium bogotense* in size or aspect. Plants of *C. haitensis*, however, are light green in color and do not grow in dense mats; they have well-spaced leaves and densely spinose setae. Microscopically, *C. haitensis* differs from *A. bogotense* in having shorter axillary hairs (2–4-celled vs. 5–12-celled) and leaves with short, double costae, thin-walled, long-hexagonal upper cells, and serrate, bordered margins. Some species of *Lepidopilum* may also resemble *A. bogotense* in size, aspect, and in having a reddish color. Plants of *Lepidopilum*, however, are usually softer than those of *A. bogotense*, and they have leaves with long, thin-walled cells and double costae.

2. *Calyptrochaeta* Desv., Mém. Soc. Linn. Paris 3: 226. 1824.

Chaetephora Brid., Muscol. Recent. Suppl. 4: 148. 1819, illegitimate homonym, not *Chaetephora* Schrank, 1783 (belongs to the algae).
Hookeria subgen. *Lophobryum* Arn., Mém. Soc. Linn. Paris 5: 297. 1826.
Chaetephora Brid. subgen. *Eriopus* Brid., Bryol. Univ. 2: 339. 1827, illegitimate name, genus a latter homonym.
Eriopus Brid., Bryol. Univ. 2: 788. 1827. *Hookeria* sect. *Eriopus* (Brid.) Müll. Hal., Syn. Musc. Frond. 2: 201. 1851.
Hookeria subgen. *Chaetephora* Endl., Gen. Pl. 56. 1836.
Piloseriopus Sharp, Hikobia 9: 305. 1986.

Plants small to large, light green to yellowish green. Stems erect to ascending, sparsely and irregularly branched, complanate-foliate, red brown below, light green above; stems in cross section with enlarged epidermal cells, cortical cells enlarged, thin-walled, central strand present; paraphyllia absent; pseudoparaphyllia subfoliose; axillary hairs 3–4 cells long; rhizoids smooth, reddish brown, from scattered initials on stems and around branch primordia, pinnately branched. Leaves somewhat dimorphic (lateral leaves asymmetric, dorsal leaves more or less symmetric), oblong-ovate, usually abruptly short-acuminate, not decurrent; margins plane, bordered by 1–3 rows of narrow, elongate, firm-walled cells, serrate above, entire to subentire below; costae short and double, occasionally reaching midleaf; upper cells hexagonal to short-rhomboidal, smooth, thin-walled; basal cells long-rectangular, 60–160 µm long; alar cells not differentiated, but sometimes with 1–3 subquadrate cells. Asexual propagula absent. Autoicous. Setae elongate, spinose below, spinose or ciliate above with 1–8-celled hairs. Capsules exserted, horizontal to pendent, ovoid to subglobose, constricted at the neck, symmetric; exothecial cells collenchymatous; stomata on neck; opercula conic-rostrate; annuli rudimentary; peristome diplolepideous; exostome teeth narrowly triangular, dorsal surface cross-striate, furrowed, trabeculae projecting laterally, median line faint; endostome yellow, lightly papillose, basal membranes high, segments keeled and perforate, cilia rudimentary or absent. Calyptrae mitrate, ciliate-fringed at base, roughened to hairy above.

Calyptrochaeta is a genus of 25 species (Crosby *et al.* 2000) principally found in the Southern Hemisphere. There are 12 species of *Calyptrochaeta* in the New World, but only one occurs in Central America. The genus, often found on rotten wood, has erect-ascending stems that are reddish brown below but light green above, with subfoliose pseudoparaphyllia, and a variably developed hyalodermis. Whittemore and Allen (1989) and Buck (1998) describe the stems as lacking a central strand, but a weakly developed central strand is present in *Calyptrochaeta*. The rhizoids of *Calyptrochaeta* originate from initials scattered on the stems or surrounding branch primordia; they are densely pinnately branched. *Calyptrochaeta* has complanate-flattened, weakly dimorphic leaves with short, double costae, smooth hexagonal to rhomboidal leaf cells, and serrate, bordered margins.

The sporophytes of *Calyptrochaeta* are distinctive in having setae that are scabrous, spinose, or have long, slender, multicellular hairs. When well developed, the hairs at the tip of the setae can be eight cells long. The capsules are pendent to inclined and have collenchymatous exothecial cells. The

peristome in *Calyptrochaeta* has strongly furrowed exostome teeth with dorsal trabeculae projecting horizontally, and although the endostome is otherwise well developed, cilia are rudimentary or absent. The calyptrae are mitrate and densely ciliate-fringed at base.

In Central America *Calyptrochaeta* is distinguished from other members of the Daltoniaceae by its short, double costae. Indeed, the genus is much more likely to be confused with *Lepidopilum*, which is gametophytically very similar. *Lepidopilum* differs from *Calyptrochaeta* in lacking a stem central strand and in having mostly unbranched rhizoids that arise from circular clusters of initials abaxial to the leaf insertions. Although the setae of *Lepidopilum* can be spinose, they are never setaceous, and its exostome teeth are mostly papillose throughout on the dorsal surface.

Calyptrochaeta appears oddly placed in the Daltoniaceae because of its weak, double costae and strongly furrowed, dorsally cross-striate exostome teeth. On the other hand, its erect-ascending, pigmented stems, intricately branched rhizoids, collenchymatous exothecial cells, and ciliate-fringed, mitrate calyptrae support the placement of the genus in the Daltoniaceae. Within the Daltoniaceae, *Calyptrochaeta* appears closest to *Acrophyllum* because both genera have: stems with a weak hyalodermis and central strand; leaves with weak, often branched costae; entirely hyaline axially hairs; and cross-striolate exostome teeth.

The name *Calyptrochaeta* combines the Greek *calyptra* (veil) with *chaete* (loose flowing hair or mane) and refers to the ciliate-fringed calyptra of the genus.

Calyptrochaeta haitensis (H. A. Crum & Steere) Crosby, Brenesia 4: 10. 1974. *Eriopus haitensis* H. A. Crum & Steere, Amer. Midl. Naturalist 60: 34. 1958. *Piloseriopus haitensis* (H. A. Crum & Steere) Sharp, Mem. New York Bot. Gard. 45: 292. 1987. Protologue. Haiti. Guimbi Galata, Morne des Commissaires, 1700–1800 m alt., *Leslie R. Holdridge 3124a, 3150a* (type), Dec. 16, 1945 (in herb. University of Michigan).

Plants small to medium-sized, 0.5–3.5 cm long, light green to yellowish green. Stems erect to ascending, sparsely and irregularly branched, complanate-foliate, red brown below, light green above; stems in cross section with moderately enlarged epidermal cells, cortical cells enlarged, thin-walled, central strand weak; paraphyllia absent; pseudoparaphyllia subfoliose; axillary hairs 3–4 cells long, basal cell short-rectangular, upper cells short and bulging, all cells hyaline; rhizoids densely felting at base of stems, smooth, reddish brown, from scattered initials on stems and around branch primordia, intricately pinnately branched. Leaves weakly dimorphic: lateral leaves wide-spreading, asymmetric, oblong-ovate, 2–3 mm long; dorsal leaves erect, more or less symmetric, oblong-ovate, 1.5–2.0 mm long. Leaves abruptly short-acuminate, not decurrent; margins plane, bordered by 1–3 rows of narrow, elongate, firm-walled cells, serrate above, entire to subentire below; costae short and double, greenish yellow, in cross section cells enlarged, firm-walled; upper cells hexagonal to long-hexagonal, smooth, thin-walled, 52–96 × 16–32 µm long; basal cells long-rectangular, 60–160 µm long; alar cells not differentiated, occasionally with 1–3 subquadrate cells. Asexual propagula absent. Autoicous. Setae elongate, curved above, 2–4 mm long, spinose below, setaceous above with 1–8-celled hairs. Capsules exserted, horizontal to pendent, ovoid to subglobose, constricted at the neck, symmetric, 1 mm long; exothecial cells enlarged, rounded to subquadrate at mouth, lower cells strongly collenchymatous; stomata on neck; opercula conic-rostrate, 0.5 mm long; annuli rudimentary; peristome diplolepideous; exostome teeth reddish yellow, narrowly triangular, dorsal surface cross-striate, strongly furrowed, trabeculae projecting laterally, median line faint; endostome yellow, lightly papillose, basal membranes high, segments keeled and perforate, cilia rudimentary or absent. Spores rounded, 10–14 µm, smooth to lightly papillose. Calyptrae mitrate, densely ciliate-fringed at base, hairy above, 1 mm long.

Illustrations. Crum and Steere (1958, Figs. 84–87); Welch (1971b, Figs. 114–122); Sharp *et al.* (1994, Fig. 581); Buck (1998, Pl. 5 5–9). Figures 129 & 130.

Habitat. On rotting logs or branches; 1750–2500 m.

Distribution in Central America. EL SALVADOR. Santa Ana: *Watson 77-01* (MO). HONDURAS. Lempira: *Allen 12181* (MO). COSTA RICA. Heredia: *Crosby & Crosby 6583* (MO); San José: *Crosby & Crosby 5960* (MO).

World range: Mexico; Central America; Caribbean.

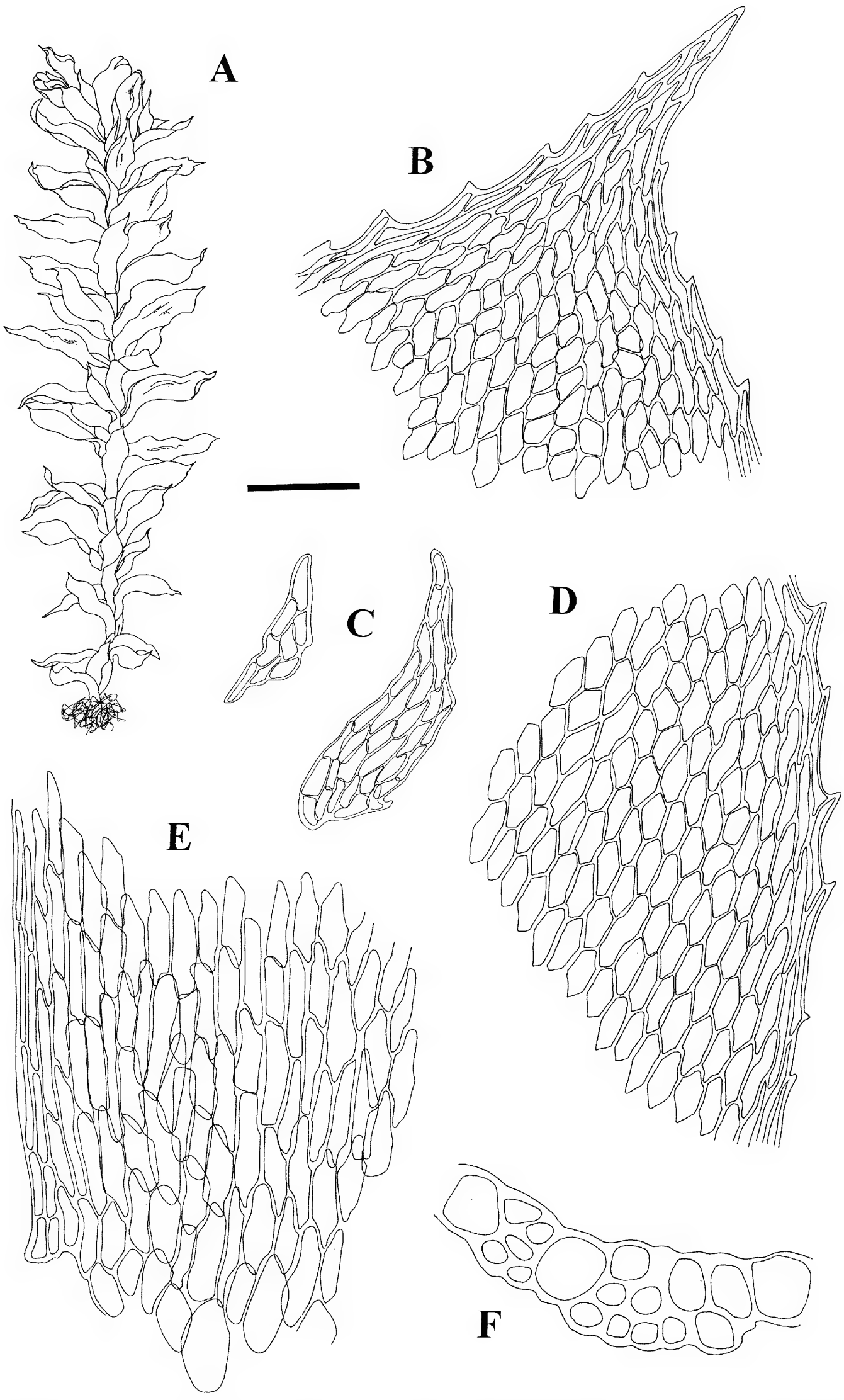


Figure 129. *Calyptrochaeta haitensis*. A. Habit. B. Leaf apex. C. Pseudoparaphyllia. D. Median leaf cells and margin. E. Basal and alar cells. F. Costa in cross section. Scale in mm: bar = 0.06 (F); bar = 0.13 (B–E); bar = 4.0 (A). A from *Crosby 13125*; C, F from *Crosby 9682*; all other figure parts from *Crosby 6583*.

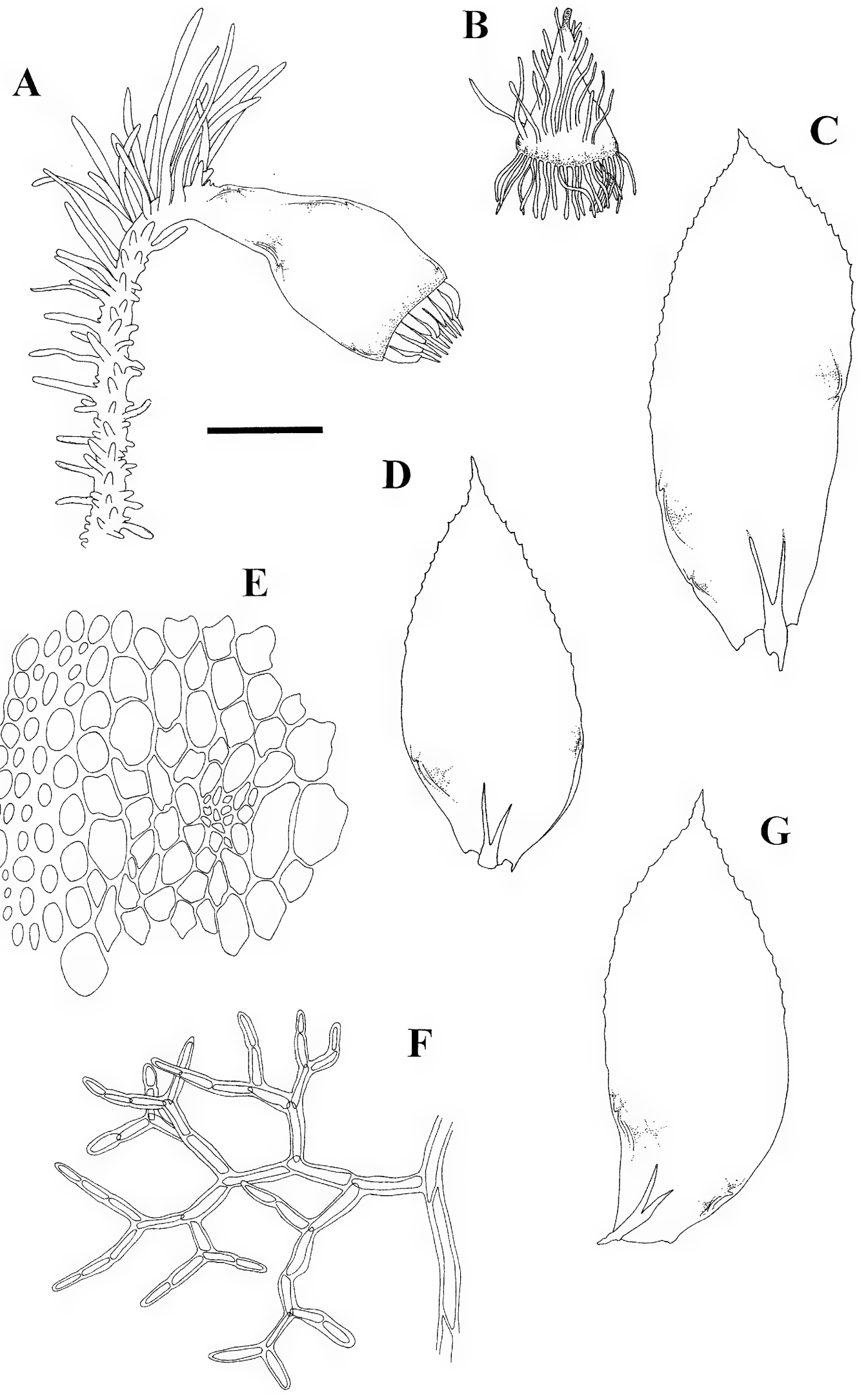


Figure 130. *Calyptrochaeta haitensis*. A. Sporophyte. B. Calyptra. C, D & G. Leaves. E. Stem in cross section. F. Rhizoids. Scale in mm: bar = 0.08 (E); bar = 0.17 (F); bar = 0.6 (A, B); bar = 0.9 (C, D, G). All figure parts from *Crosby 6583*.

Calyptrochaeta haitensis is a small to medium-sized species restricted in Central America to logs and rotting branches at high elevations. The plants grow erect to ascending from a dense rhizoidal mass with stems that are reddish brown at base but light greenish above. The rhizoids in *C. haitensis* arise from initials scattered on the stem or around branch primordia, and they are densely pinnately branched. Although not previously noted, Central American plants of *C. haitensis* have a weakly developed stem central strand and subfoliose pseudoparaphyllia. *Calyptrochaeta haitensis* has flattened, dimorphic leaves that are only lightly contorted when dry. Its leaves are oblong-ovate, but the lateral leaves are asymmetric, while the ventral leaves are somewhat smaller and symmetric. The leaf apices are abruptly short-acuminate, the costae very short and double, and the margins bordered throughout as well as serrate above. The leaf cells are large, thin-walled, and mostly long-hexagonal, with not or faintly differentiated alar cells. Sporophytically, *Calyptrochaeta haitensis* is quite distinctive. The setae are elongate, strongly curved just below the capsule, and spinose at base but beset above by long, multicellular hairs. The capsules are constricted at base, with exothecial cells enlarged in several rows at the capsule mouth and strongly collenchymatous below. Its peristome has exostome teeth densely cross-striate throughout and broadly furrowed on the dorsal surface, with the trabeculae strongly projecting horizontally; the endostome is well developed, but has rudimentary cilia. The calyptrae are mitrate, hairy, and densely ciliate-fringed at base.

Within Central American Daltoniaceae only *Adelothecium bogotense* is comparable to *Calyptrochaeta haitensis* in size and aspect. Plants of *A. bogotense*, however, are often yellowish red in color, they grow in dense mats, and they have numerous rhizoids along the stems, closely spaced leaves, and smooth or at best lightly roughened setae. Microscopically, *A. bogotense* differs from *C. haitensis* in having longer axillary hairs (5–12-celled vs. 2–4-celled) and leaves with long, single costae, oval to oblong, thick-walled, collenchymatous, and porose cells, and denticulate-crenulate, unbordered margins. *Calyptrochaeta haitensis* is much more likely to be confused with species of *Lepidopilum*, which resemble it in size, aspect, cellular areolation, costal form, leaf margin form, and coloration. *Lepidopilum* differs from *Calyptrochaeta haitensis* in lacking a stem central strand and in having mostly unbranched rhizoids that arise from circular clusters of initials abaxial to the leaf insertions. Although the setae of *Lepidopilum* can be spinose they are never setaceous, and its exostome teeth are mostly papillose throughout on the dorsal surface.

3. *Daltonia* Hook. & Taylor, Muscol. Brit. 80: 1818. *Neckera* Hedw. sect. *Daltonia* (Hook. & Taylor) Wallr., Fl. Crypt. Germ. 1: 217. 1831.

Plants small to medium-sized, glossy, yellowish green. Stems erect, sparsely and irregularly branched, evenly foliate, dark red; stems in cross section with hyalodermis of enlarged, red, often porose cells, subepidermis with small, thick-walled, red cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2–4 cells long; basal cells short-rectangular, reddish brown, upper cells oblong-elongate, hyaline; rhizoids at base of stems, around branch primordia, and along stems abaxial to the leaf insertions, smooth, reddish brown, at times pinnately branched. Leaves isophyllous, erect, flexuose-twisted, or spirally contorted when dry, erect, erect-spreading, or erect-flexuose when wet, oblong-ligulate, narrowly ovate, oblong- or ovate-lanceolate, lanceolate or linear-lanceolate, keeled below, acute to acuminate, decurrent; margins plane or narrowly recurved, bordered by elongate, thick-walled cells, entire or minutely denticulate near the apex; costae single, strong, often flexuose, ending 3/4 the leaf length, in cross section cells homogeneously thick-walled; upper cells oval-hexagonal, rhombic, oblong, narrowly rhomboidal, fusiform, or elongate-fusiform, smooth; basal cells oblong, rectangular, long-rectangular to linear, firm-walled or lax and bulging, juxtacostal cells at times linear, similar to the border cells, cells across the insertions enlarged, irregularly rectangular to subquadrate, reddish brown, porose. Asexual reproduction occasionally by multicellular, uniseriate, clavate to fusiform propagula, abaxial at the base of the costa. Autoicous or synoicous. Perichaetia and perigonia lateral on stems. Setae elongate, red, scabrose or smooth. Capsules erect, or slightly inclined, ovoid to oblong, more or less constricted at the neck, symmetric; exothecial cells at the mouth oblate, lower cells larger, oblate, rounded-quadrate, or subrectangular, collenchymatous; stomata on neck; opercula conic-rostrate; annuli rudimentary, persistent; peristome diplolepideous; exostome teeth reddish yellow at base, recurved when wet, incurved when dry, narrowly triangular, both surfaces papillose throughout, dorsal trabeculae

and median line thick, ventral trabeculae faint; endostome yellowish white, spiculose-papillose above, basal membranes low, segments linear, not keeled, not or faintly perforate, cilia absent. Calyptrae mitrate, densely ciliate-fringed at base, naked, smooth or lightly roughened above.

Daltonia is a genus of 60 species, only 31 of which are reasonably well known (Crosby *et al.* 2000). It is epiphytic and is found throughout the tropics at mostly high elevations. *Daltonia* often occurs on twigs in the canopy; its plants are glossy and yellowish green, with erect, sparsely branched stems. Many herbarium collections of *Daltonia* contain more than one species of *Daltonia*, but this does not necessarily indicate the species occur as intermixed populations. *Daltonia* usually grows in small, isolated tufts, and collectors tend to place material from nearby twigs or branches in the same collection bag. As a result, mixed herbarium collections likely represent poor collection technique rather than intermixed populations. *Daltonia* stems and branches have an enlarged hyalodermis that consists of dark red cells with 1–2 large pores. There is no stem central strand, and the branch buds are naked. Although rhizoids are sparsely developed on most plants of *Daltonia*, when present they are pinnately branched. *Daltonia* has lanceolate leaves that are mostly erect-flexuose or erect-contorted when dry and that have strong single costae, well-developed borders of elongate, linear cells, and smooth cells. Propagula are often present at the base of the costae on the abaxial side of the leaves.

Daltonia species are autoicous or synoicous, and sporophytes are commonly encountered in the field. Due to the sparse and scattered habit of its plants, the presence of sporophytes greatly aids in the field recognition of the genus. The sporophytes of *Daltonia* have long setae, erect, ovoid to oblong, usually symmetric capsules, with collenchymatous exothecial cells, and short-rostrate opercula. *Daltonia* has a diplolepideous peristome with reddish brown to yellowish exostome teeth that are papillose throughout on both surfaces. The exostome teeth are hygrocastique: recurved when wet, erect or incurved when dry. They have reduced endostomes with low basal membranes, linear non-keeled segments that are faintly perforate, and no cilia. The calyptrae are mitrate and densely ciliate-fringed at base.

The Neotropical species of *Daltonia* were reviewed by Bartram (1931). This treatment is still very useful; however, the species in this review were narrowly defined because of the small amount of material available for the study. In addition, the illustrations often fail to convey the habit and critical basal leaf cell differences between the species.

The name *Daltonia* honors the Rev. James Dalton, Rector of Croft, in Yorkshire, and godfather of Joseph Dalton Hooker (see J. Bot. 50: 6. 1912). James Dalton was also a British botanist and bryologist (Bartram 1931; Dixon 1904).

1. Leaf margins typically plane, occasionally broadly reflexed below 2
1. Leaf margins narrowly and tightly revolute 3

2. Upper leaf cells rhombic, 10–14 × 6–10 µm; basal cells oblong to rectangular, enlarged and bulging, 30–60 × 8–12 µm . . . . . 6. *D. pulvinata*
2. Upper leaf cells oval-oblong, 14–26 × 6 µm; basal cells narrowly oval to linear-rhomboidal, firm-walled, not bulging, 16–30 × 4–8 µm . . . . . 4. *D. longifolia*

3. Basal juxtacostal leaf cells elongate, thick-walled, similar to the border cells 4
3. Basal juxtacostal leaf cells not strongly differentiated or similar to the border cells 5

4. Elongate juxtacostal cells extending from base to midleaf or above, contrasting sharply with inner basal cells . . . . . 1. *D. gomezii*
4. Elongate juxtacostal cells restricted to the base, inner basal cells elongate and grading into the border cells . . . . . 3. *D. lindigiana*

5. Basal cells linear with tapered ends; border indistinct below . . . . . 7. *D. stenophylla*
5. Basal cells oblong with truncate or rounded ends; border distinct below 6

6. Plants medium-sized; leaves oblong-lanceolate, 0.5–0.8 mm wide at base; border 10–15 cells wide at base . . . . . 5. *D. peruviana*
6. Plants small; leaves linear-lanceolate, lanceolate, or oblong-ligulate, 0.3–0.4 mm wide at base; border 4–8 cells wide at base 7

7. Leaves oblong-ligulate, spirally twisted around stem when dry; basal cells short-oblong to subrectangular . . . . . 9. *D. trachyodonta*
7. Leaves linear-lanceolate or lanceolate, erect, flexuose-twisted when dry; basal cells linear-oblong 8

8. All basal leaf cells thin-walled and bulging . . . . . 8. *D. tenuifolia*
8. Basal leaf cells near costa at times bulging but outer cells firm-walled or cells firm-walled throughout . . . . . 2. *D. gracilis*

1. *Daltonia gomezii* Crosby, Brenesia 4: 10. 1974. Protologue. Costa Rica. Cartago: along Inter-American Highway. Bamboo brake about 8 kilometers NW of summit at La Ascención. 3200 meters. 0.37 [sic] N; 83.47 W. 15.iii.1973. *Crosby & Crosby 6130*. Type. Costa Rica. Cartago: along Inter American Highway. Bamboo brake about 8 km NW of summit at La Ascención. 3200 m. 9.37 N; 83.47 W. 15.iii.1973. *Crosby & Crosby 6130*. (MO, holotype).

Plants medium-sized, 1.0–3.5 cm long, glossy, yellowish green. Stems erect, sparsely and irregularly branched, evenly foliate, dark red; stems in cross section with hyalodermis of enlarged, reddish cells, subepidermis of 1–3 rows of small, thick-walled, red cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2 cells long, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids at base of stems, around branch primordia, and at times along the stems, smooth, reddish brown, from initials abaxial to the leaf insertions and from scattered initials, at times pinnately branched. Leaves isophyllous, laxly erect-imbricate, somewhat flexuose when dry, erect-spreading when wet, narrowly ovate to oblong-lanceolate, 2.5–3.0 mm long, 0.5–0.9 mm wide at base, deeply keeled in lower 1/2, acute to somewhat acuminate, decurrent; margins narrowly recurved, bordered by elongate, thick-walled cells, 8–11 cells wide below, entire throughout, rarely minutely denticulate near the apices; costae single, strong, often flexuose, ending 3/4 the leaf length, in cross section cells homogeneously thick-walled; upper cells rounded-rhomboidal to elongate-fusiform, 18–35 × 7–10 µm, smooth, firm-walled, median cells similar but somewhat larger; basal cells rounded-rectangular, firm-walled, 18–40 × 7–12 µm, juxtacostal cells linear, similar to the border cells, forming a distinct band along the costa from the base into the apex, cells across the insertions enlarged, irregularly rectangular to subquadrate, reddish brown, porose. Asexual structures not seen. Autoicous. Perichaetia lateral on stems. Setae elongate, 10–12 mm long, red, scabrose above, smooth below. Capsules erect, ovoid to oblong, more or less constricted at the neck, symmetric, 1.0–1.5 mm long; exothecial cells at the mouth oblate in 3–4 rows, lower cells larger, oblate, rounded-quadrate, or subrectangular, collenchymatous; stomata on neck; operculum and annulus not seen; peristome diplolepideous; exostome teeth reddish yellow at base, recurved when wet, incurved when dry, narrowly triangular, both surfaces papillose throughout, dorsal trabeculae and median line thick, ventral trabeculae faint; endostome yellowish white, spiculose-papillose above, basal membranes low, segments linear, not keeled, not or faintly perforate, cilia absent. Spores rounded, 15–20 µm, lightly papillose. Calyptra not seen.

Illustrations. Crosby (1974a, Fig. 1). Figure 131.

Habitat. On tree branches and bamboo; 3130–3200 m.

Distribution in Central America. COSTA RICA. Cartago: *Crosby & Crosby 6130* (MO); San José: *Crosby & Crosby 5830A* (MO).

World range: Central America; Western and Northern South America.

Daltonia gomezii is a medium-sized species with large, narrowly ovate to oblong-lanceolate leaves that are imbricate-erect to somewhat flexuose when dry. The leaves have tightly recurved margins and well-developed borders that near the base are 8–11 linear cells wide. The upper leaf cells are usually rounded-rhomboidal, but sometimes they can be elongate-fusiform. The basal cells are oblong to variously rectangular (sometimes more or less quadrate), firm to bulging, and hyaline. The most distinctive feature of *D. gomezii* is the presence of a broad band of elongate to linear cells along the costae that extend from the leaf base well into the apex. These cells are similar to the border cells, and two bands of linear cells enclosing the short, enlarged, hyaline basal leaf cells give the leaf base

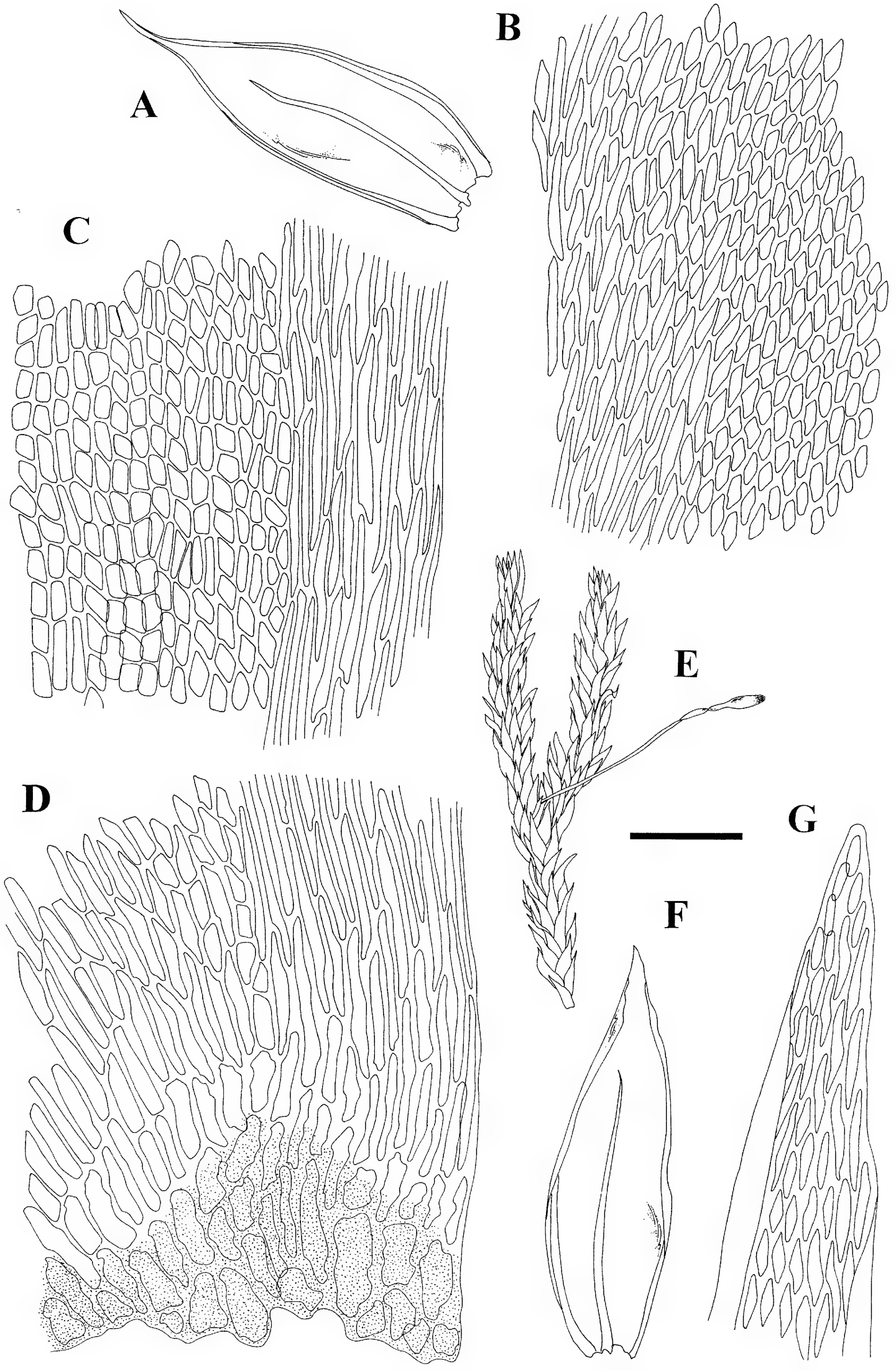
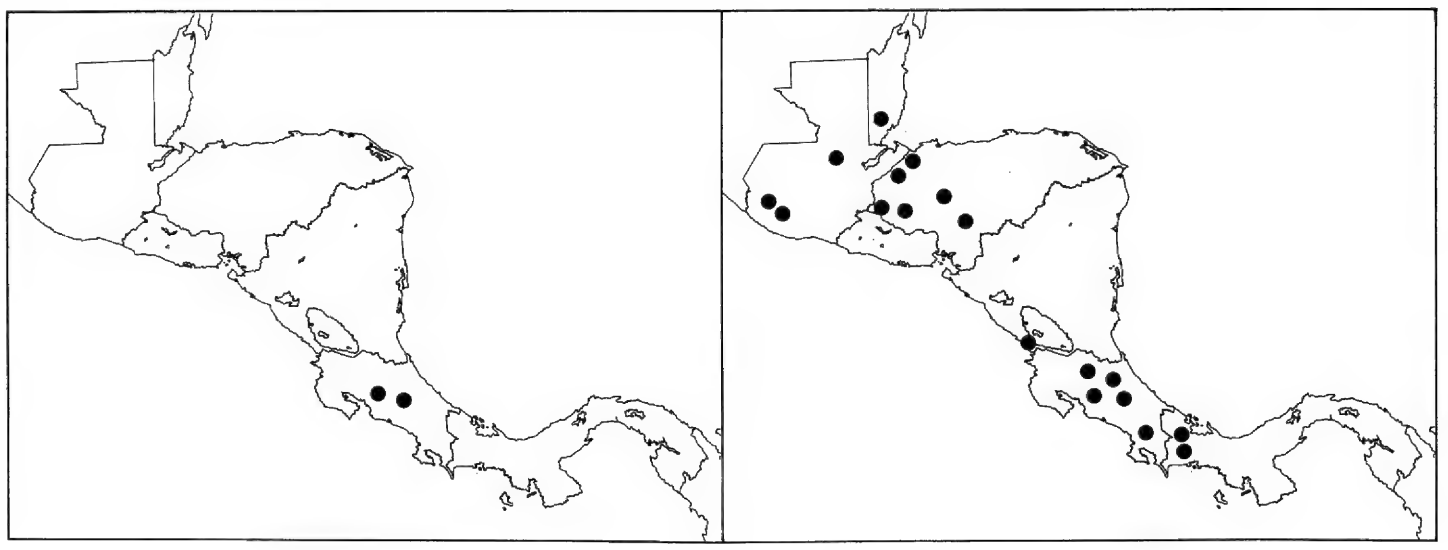


Figure 131. *Daltonia gomezii*. A & F. Leaves. B. Upper leaf cells showing elongate juxtacostal cells. C. Lower leaf cells and margin. D. Basal and alar cells. E. Habit. G. Leaf apex. Scale in mm: bar = 0.06 (B–D); bar = 0.9 (A, F); bar = 5.0 (E). All figure parts from *Crosby & Crosby 6130* (type).



Daltonia gomezii *Daltonia gracilis*

a distinctive appearance. *Daltonia gomezii* has long setae that were originally reported as smooth throughout. The setae in the type collection, however, are lightly papillose below the capsules.

This is the only Central American species of *Daltonia* with elongate juxtacostal cells. There are two South American species with this feature: *D. latolimbata* Herzog and *D. brevinervis* E. B. Bartram (*Daltonia fenestrellata* Griffin is a synonym of *D. brevinervis*; see Churchill *et al.* 2000). I have not seen the types of *D. brevinervis* or *D. latolimbata*, but on the basis of their descriptions the three species can be separated in the following way. *Daltonia brevinervis* has acute leaves, linear upper leaf cells, leaf borders 6–8 cells wide at base, and setae scabrose. *D. gomezii* has acute or slightly acuminate leaves, rhomboidal upper leaf cells, leaf borders 8–11 cells wide at base, and setae smooth to lightly papillose. *Daltonia latolimbata* has acuminate leaves, oval upper leaf cells, leaf borders 12–15 cells wide at base, and setae lightly roughened above. The upper leaf cells within this complex appear to be a highly variable feature both within and between collections. All three taxa have similar basal leaf cells, and it seems likely *D. gomezii* will become a synonym of either *D. brevinervis* or *D. latolimbata*.

2. *Daltonia gracilis* Mitt., J. Linn. Soc., Bot. 12: 402. 1869. Protologue. [Ecuador] Andes Quitenses, in sylva Canelos, ad folia et ramulos praecipue Bambusarum (3000 ped.), *Spruce, n. 560*. Type. M. de Canelos, *Spruce 560* (NY, holotype).

Plants small, 0.3–1.0 cm tall, glossy, green to yellowish green. Stems erect, sparsely and irregularly branched, evenly foliate, dark red; stems in cross section with 1–2 rows of enlarged, reddish hyalodermis cells sometimes with a central pore, subepidermis of 1–2 rows of small, firm- to thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 3–4 cells long, basal 1–2 cells short-rectangular, reddish brown, upper cells oblong-elongate, hyaline; rhizoids at base of stems, around branch primordia, and along the stems, smooth, reddish brown, from scattered initials, weakly branched, branches with transverse cross-walls. Leaves isophyllous, erect, flexuose-twisted when dry, erect to erect-spreading, somewhat flexuose when wet, lanceolate to linear-lanceolate, 2–3 mm long, often keeled in lower 1/2, narrowly acuminate, decurrent; margins narrowly revolute on one or both sides, often plane at the extreme base, bordered by elongate, thick-walled, sometimes porose cells, (4–)5–8 cells wide at base, entire; costae single, strong, often flexuose, ending 3/4–7/8 the leaf length, in cross section cells homogeneously thick-walled; upper cells rhombic, oblong, narrowly rhomboidal, or fusiform, 12–26 × 6 μm, smooth, median cells at times a little longer, otherwise similar; basal cells oblong, rectangular, long-rectangular to linear, firm-walled, not or weakly bulging, 24–50 × 6–10 μm; alar cells not differentiated, cells across the insertions enlarged and reddish. Asexual reproduction occasionally by multicellular, uniseriate, clavate to fusiform propagula, abaxial at the base of the costa. Autoicous or synoicous. Perichaetia lateral on stems. Setae elongate, 4–10 mm long, red, scabrose above, smooth or roughened below. Capsules erect or slightly inclined, ovoid to oblong, more or less constricted at the neck, sym-

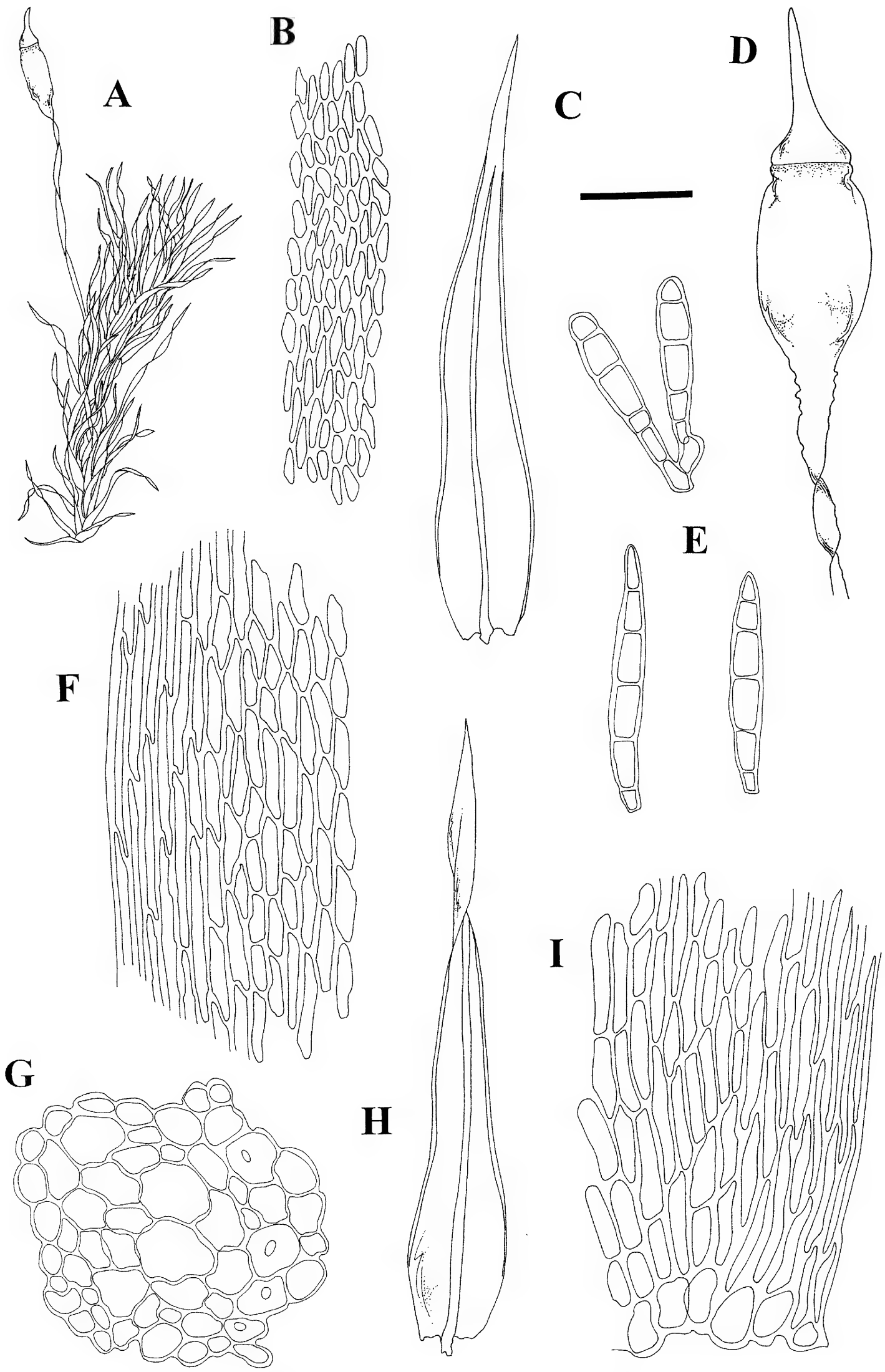


Figure 132. *Daltonia gracilis*. A. Habit with sporophyte. B. Upper leaf cells. C & H. Leaves. D. Seta, capsule, and operculum. E. Gemmae. F. Upper basal leaf cells and margin. G. Stem in cross section. I. Basal and alar cells. Scale in mm: bar = 0.06 (B, E, F, I); bar = 0.08 (G); bar = 0.5 (C, D, H); bar = 2.0 (A). All figure parts from *Crosby 9816*.

metric, 1.0–1.5 mm long; exothecial cells at the mouth oblate in 3–4 rows, lower cells larger, oblate, rounded-quadrate, or subrectangular, collenchymatous; stomata on neck; opercula conic-rostrate, 0.7–1.0 mm long; annuli rudimentary, persistent; peristome diplolepideous; exostome teeth yellow, recurved when wet, incurved when dry, linear-triangular, both surfaces papillose throughout, dorsal trabeculae and median line thick, ventral trabeculae faint; endostome yellowish white, papillose throughout, basal membranes low, segments linear, not keeled, not or faintly perforate, cilia absent or rudimentary. Spores rounded, 10–16 µm, lightly papillose. Calyptrae mitrate, densely ciliate-fringed at base, naked, smooth or lightly roughened above, 1–1.5 mm long.

Illustrations. Bartram (1931, Pl. 4 17); Bartram (1949, Fig. 131 I & J); Welch (1966, Figs. 122–130); Sharp *et al.* (1994, Fig. 576, Fig. 577, as *D. stenophylla*); Churchill and Linares (1995, Fig. 56 a–f). Figure 132.

Habitat. On twigs, small tree trunks, branches, shrubs, bamboo nodes, and leaves, occasionally on rotting wood or rocks near streams; 685–3330 m.

Distribution in Central America. BELIZE. Toledo: *Allen 18677* (MO). GUATEMALA. Alta Verapaz: *Svihla 2885b* (FH); Quetzaltenango: *Sharp* 5070 (NY, TENN); Suchitepéquez: *Standley 66941a* (F, FH). HONDURAS. Comayagua: *Allen 12301* (MO); Cortés: *Allen 14085* (MO); Francisco Morazán: *Standley 14797* (F, mixed with *D. longifolia*); Lempira: *Allen 12008A* (MO); Ocotepeque: *Allen 14441* (MO); Santa Bárbara: *Allen 11668* (MO). NICARAGUA. Rivas: *B. S., 1893* (FH). COSTA RICA. Alajuela: *Crosby & Crosby 5896* (MO); Cartago: *Crosby & Crosby 5912* (MO); Heredia: *Crosby & Crosby 5996* (MO); Puntarenas: *Lyon 351* (MO); San José: *Crosby 9816* (MO). PANAMA. Bocas del Toro: *Allen 5249A* (MO); Chiriquí: *Allen 9160A* (MO).

World range: Southwestern U.S.A.; Mexico; Central America; Western, Northern, and Southern South America; Brazil.

Daltonia gracilis is one of the most common *Daltonia* species in Central America. The species often occurs in mixed collections with other *Daltonia* species; it has been found with *D. longifolia*, *D. stenophylla*, *D. gomezii*, *D. peruviana*, and *D. trachyodonta*. As noted previously, however, this may indicate poor collection technique rather than a true association. Plants of *D. gracilis* are medium-sized to slender, and its erect stems grow in both small, isolated patches and extensive mats. They are typically erect to flexuose-twisted when dry, but occasionally the stems are lightly spirally twisted. The lanceolate to linear-lanceolate leaves are narrowly acuminate and have distinct marginal borders that are mostly 5–8 cells wide at the base. While the margins are narrowly revolute on one or both sides, they typically are plane at the very base. The upper and median leaf cells are rhombic to narrowly rhomboidal or fusiform, and they contrast strongly with the basal cells, which are generally firm-walled, oblong to long-rectangular, or sometimes linear. The form of the basal leaf cells is a critical feature of the species, and occasionally they can be weakly bulging. In order to correctly interpret this feature, several leaves should be examined. Asexual propagula have not previously been reported for *D. gracilis*, but they often occur on the abaxial side of the leaf at the base of the costae. The setae of *D. gracilis* are 4–10 mm in length and consistently scabrose above. Although the lower parts of the setae are mostly smooth, occasionally they can be papillose-roughened. Its erect, symmetric capsules have numerous stomata at their constricted neck, and the exothecial cells are strongly collenchymatous.

Daltonia gracilis belongs to the Central American *Daltonia* group with tightly revolute leaf margins. It differs from most members of the group in its smaller size and in having linear-lanceolate to lanceolate leaves. In Central America it can be confused with *D. stenophylla* or *D. tenuifolia*, which are similar to *D. gracilis* in size, leaf stance, and in having linear-lanceolate to lanceolate leaves. *Daltonia stenophylla* differs from *D. gracilis* in having linear basal leaf cells that are often tapered at the ends. Furthermore, the basal leaf cells grade more or less smoothly into the marginal cells, making it hard to distinguish the basal cells from the marginal cells. *Daltonia tenuifolia* differs from *D. gracilis* in having thin-walled, bulging basal leaf cells and smooth setae. In older material of *D. tenuifolia* the thin-walled basal cells collapse when dry and often fail to expand when re-hydrated. The European *D. splachnoides* (Sm.) Hook. & Taylor is extremely close to *D. gracilis*. It differs from *D. gracilis* in having enlarged and bulging basal, juxtacostal cells. Although most Central American collections of

D. gracilis have firm-walled basal cells, as noted above there are occasional collections that have weakly bulging basal juxtacostal cells. Otherwise, the two species appear to be identical.

3. *Daltonia lindigiana* Hampe, Ann. Sci. Nat., Bot., sér. 5, 4: 363. 1866. Protologue: [Colombia] Bogotá, Boquerón, 2700 m, ad rupes humid. Julio 1859, sub *n° 2023* leg. *Lindig*.

Daltonia irrorata Mitt., J. Linn. Soc., Bot. 12: 399. 1869. Protologue. [Colombia] Andes Bogotenses, Boquerón prope Bogotá infra rupium stillicidia, ad ramulos emortuos saxaque (8500 ped.), *Weir, n. 193, 294, 329, 336, 338.*

Daltonia stewartii R. S. Williams, Bryologist 27: 38. 1924. Protologue. [Ecuador, Galapagos Islands] Chatham Island [*Alban Stewart*] *2782.*

Plants medium-sized, 1–5 cm tall, glossy, green to yellowish green. Stems erect, sparsely and irregularly branched, evenly foliate, dark red; stems in cross section with hyalodermis of enlarged, reddish, at times pored cells, subepidermis of 1–3 rows of small, thick-walled, red cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 3–4 cells long, basal 1–2 cells short-rectangular, reddish brown, upper cells oblong-elongate, hyaline; rhizoids smooth, reddish brown, at times pinnately branched, at base of stems, around branch primordia, and along the stems abaxial to the leaf insertions. Leaves isophyllous, erect, straight or somewhat flexuose when dry, erect-spreading to spreading when wet, lanceolate to narrowly lanceolate, 3–4 mm long, deeply keeled in lower 1/2, acuminate, decurrent; margins narrowly recurved, bordered by elongate, thick-walled, sometimes porose cells, 8–10 cells wide at base, entire throughout or minutely denticulate near the apices; costae single, strong, often flexuose, ending 7/8 the leaf length, in cross section cells homogeneously thick-walled; upper cells narrowly rhomboidal to elongate, 25–50 × 5–86 µm, smooth, sometimes porose, median cells longer, otherwise similar, interior basal cells linear-rhomboidal to linear, firm-walled, not bulging, often porose, to 60 µm long, juxtacostal basal cells in a broad band similar to border cells and grading into the interior basal cells, cells across the insertions enlarged, reddish, porose. Asexual reproduction occasionally by multicellular, uniseriate, clavate to fusiform propagula, abaxial at the base of the costa. Autoicous. Perichaetia lateral on stems. Setae elongate, 5–12 mm long, red, scabrose above, smooth or roughened below. Capsules erect, ovoid to oblong, more or less constricted at the neck, symmetric, 1.0–1.25 mm long; exothecial cells at the mouth oblate in 3–4 rows, lower cells larger, oblate, rounded-quadrate, or subrectangular, collenchymatous; stomata on neck; opercula conic-rostrate, 0.7–1.0 mm long; annuli rudimentary, persistent; peristome diplolepideous; exostome teeth reddish yellow at base, narrowly triangular, both surfaces papillose throughout, dorsal trabeculae and median line thick, ventral trabeculae faint; endostome yellowish white, papillose throughout, basal membranes low, segments linear, not keeled, not or faintly perforate, cilia absent. Spores rounded, 12–18 µm, lightly papillose. Calyptrae mitrate, densely ciliate-fringed at base, naked, smooth or lightly roughened above, 1.0–1.5 mm long.

Illustrations. Williams (1924, Pl. 7); Bartram (1931, Pl. 3 9); Welch (1974, Figs. 125–133). Figure 133.

Habitat. On twigs and small trees; 2680–3200 m.

Distribution in Central America. COSTA RICA. Cartago: *Crosby & Crosby 8582* (MO).

World range: Central America; Western South America.

Daltonia lindigiana is a medium-sized species, with lanceolate leaves that are stiffly erect when dry and variously spreading when wet. It is similar to *D. longifolia* in size and overall aspect, but it belongs to the *Daltonia* group with narrowly recurved margins. The leaves have broad, well-developed borders. The basal cells of *D. lindigiana* are unusual in having a broad band of juxtacostal cells that are more or less identical to the border cells, and elongate interior basal cells. In most leaves the juxtacostal basal cells grade into the interior cells, which in turn merge into the border cells. As a result it can be difficult to determine where the border ends and the basal cells begin. The upper and median leaf cells are variable in shape but relatively long for the genus, and there are usually some nearly linear cells.

Bartram (1931) compared *D. lindigiana* to *D. stenophylla*, which is a much smaller species with narrow, linear-lanceolate leaves that are only 0.3 mm wide and with linear basal leaf cells. The spe-

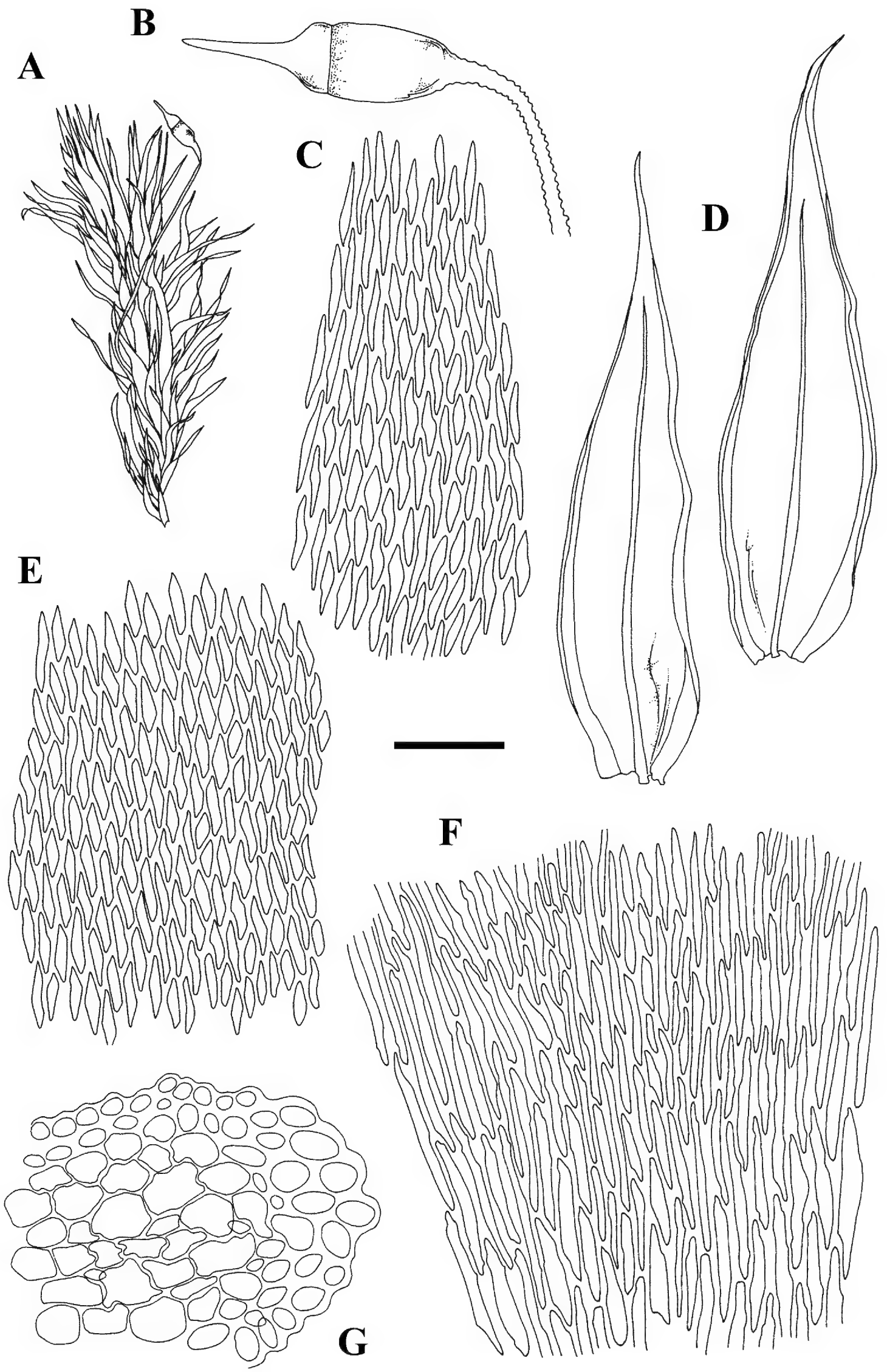
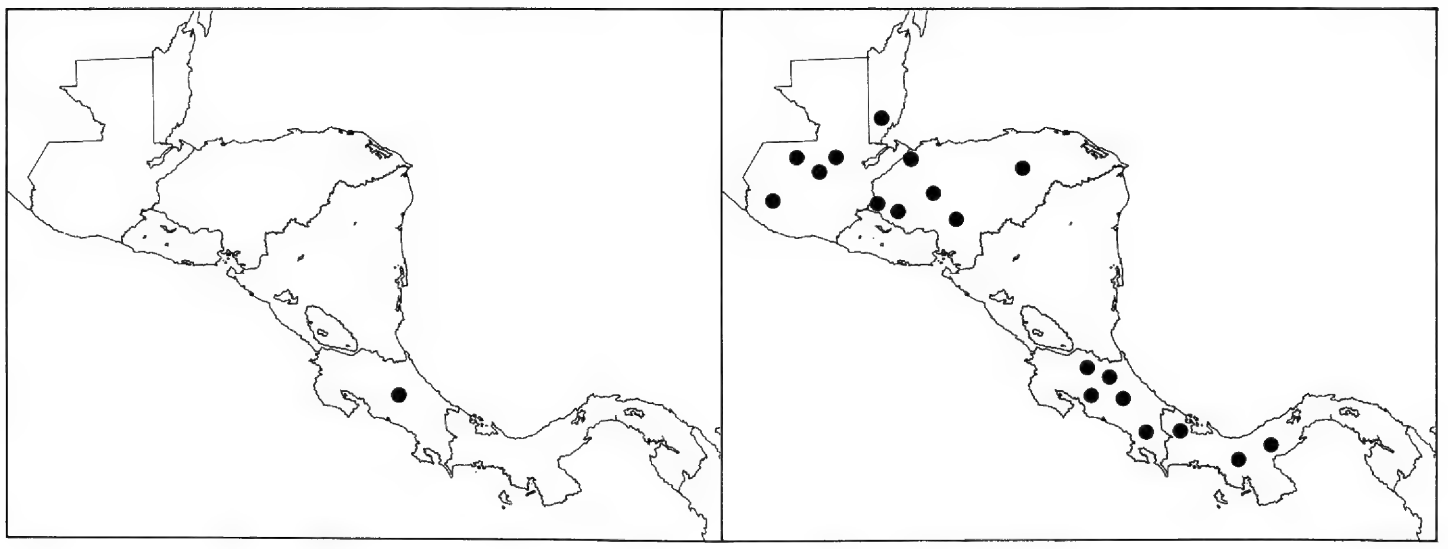


Figure 133. *Daltonia lindigiana*. A. Habit. B. Seta, capsule, and operculum. C. Upper cells. D. Leaves. E. Median leaf cells. F. Basal leaf cells. G. Stem in cross section. Scale in mm: bar = 0.06 (C, E, F); bar = 0.08 (G); bar = 0.71 (B, D); bar = 3.2 (A). All figure parts from *Crosby & Crosby 8582*.



Daltonia lindigiana *Daltonia longifolia*

cies, however, is more closely aligned with the *Daltonia* group that has juxtacostal cells more or less identical to the border cells: *D. gomezii*, *D. latolimbata*, and *D. brevinervis*. All four species are similar in size and in overall aspect. The other members of the group differ from *D. lindigiana* in having short interior basal leaf cells that sharply contrast with the border, and basal juxtacostal cells.

4. *Daltonia longifolia* Taylor, London J. Bot. 7: 284. 1848. Protologue. [Ecuador] On Pichincha. *Prof. W. Jameson*. Feb., 1847.

Daltonia crispata Schimp. *ex* Besch., Mém. Soc. Sci. Cherbourg 16: 228. 1872. Protologue. In Mexico (*Sallé*).

Daltonia robusta Ångstr., Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 1873: 117. 1873. Protologue. [Ecuador, Galapagos Islands] Charles-ön (Galapagos-öarne) [*N. J. Andersson*].

Daltonia dussii Broth. *in* Urb., Symb. Antill. 3: 426. 1903. Protologue. Martinique, inter Ajoupa et Bouillon ad ramulos arborum rarissima: *Duss n. 345* (in Herb. Berol.).

Daltonia brevicuspidata Broth. *in* E. B. Bartram, Bull. Torrey Bot. Club 58: 47. 1931, invalid name, listed in synonymy.

Plants medium-sized, 1–4 cm tall, glossy, green to yellowish green. Stems erect, sparsely and irregularly branched, evenly foliate, dark red; stems in cross section with hyalodermis of enlarged, reddish cells, subepidermis of 1–3 rows of small, thick-walled, red cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 3–4 cells long, basal 1–2 cells short-rectangular, reddish brown, upper cells oblong-elongate, hyaline; rhizoids dense at base of stems and around branch primordia, and at times scattered along the stems, smooth, reddish brown, from single initial or chains of initials on or abaxial to the leaf insertions and from scattered initials, at times pinnately branched. Leaves isophyllous, spirally contorted when dry, erect-flexuose when wet, lanceolate to ovate-lanceolate, 2.0–3.5 mm long, often deeply keeled in lower 1/2, sharply acuminate, decurrent; margins plane, bordered by elongate, thick-walled, sometimes porose cells, 6–12 cells wide at base, entire throughout or minutely denticulate near the apices; costae single, strong, often flexuose, ending 7/8 the leaf length, in cross section cells homogeneously thick-walled; upper cells oval-oblong, 14–26 × 6 µm, smooth, sometimes porose, median cells similar, at times in oblique rows; basal cells narrowly oval to linear-rhomboidal, firm-walled, not bulging, often porose, 16–30 × 4–8 µm; alar cells not differentiated, cells across the insertions enlarged, reddish, porose. Asexual reproduction occasionally by multicellular, uniseriate, clavate to fusiform propagula, abaxial at the base of the costa. Autoicous or synoicous. Perichaetia lateral on stems. Setae elongate, 3–10 mm long, red, scabrose above, smooth below. Capsules erect, ovoid to oblong, more or less constricted at the neck, symmetric, 1.0–1.5 mm long; exothecial cells at the mouth oblate in 3–4 rows, lower cells larger, oblate, rounded-quadrate, or subrectangular, collenchymatous; stomata on neck; opercula conic-rostrate, 0.7–1.0 mm long; annuli rudimentary, persistent; peristome diplolepideous; exostome teeth reddish yellow at base, recurved when wet, incurved when dry, narrowly triangular, both

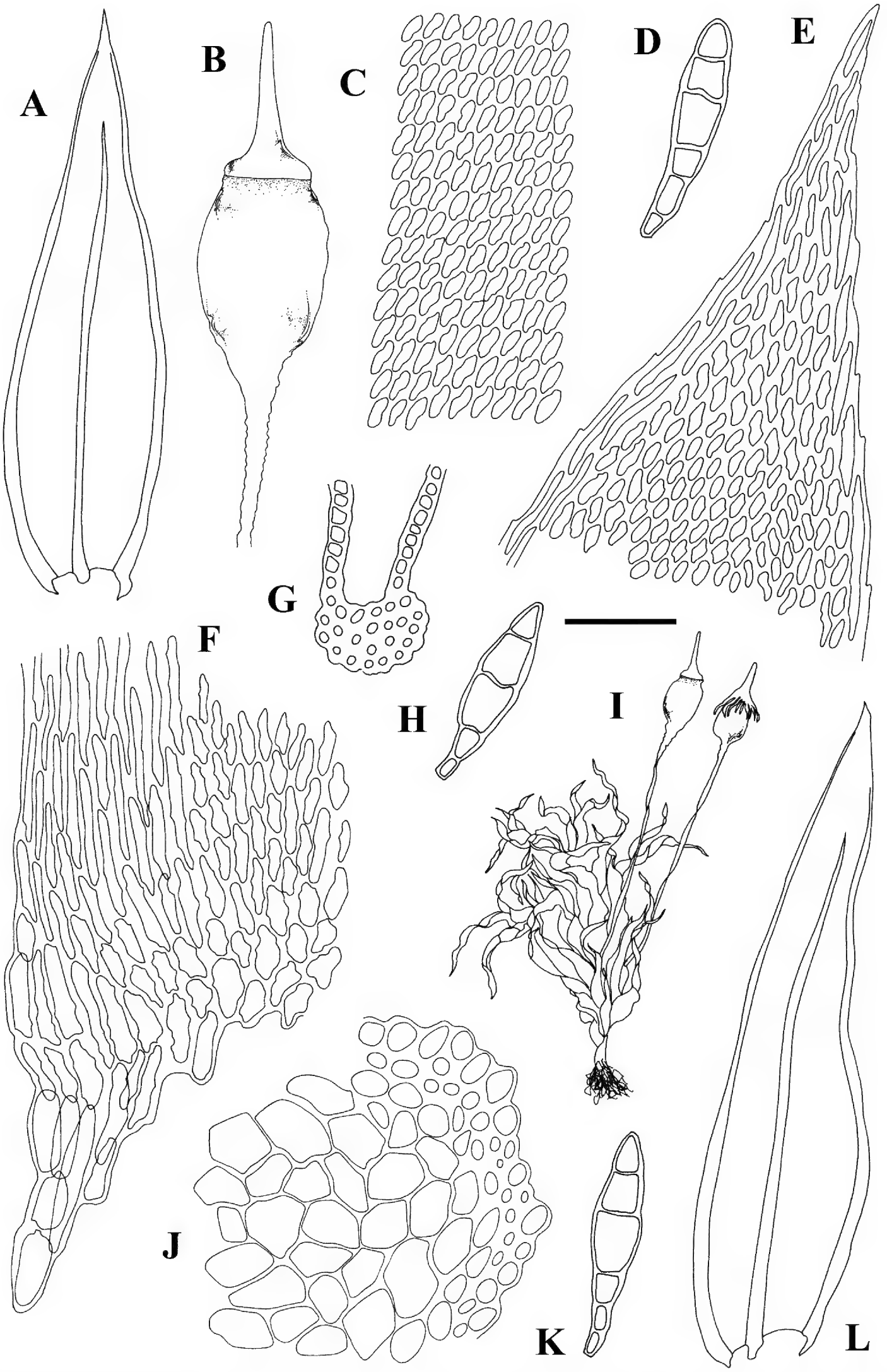


Figure 134. *Daltonia longifolia*. A & L. Leaves. B. Seta, capsule, and operculum. C. Median leaf cells. D, H & K. Gemmae. E. Leaf apex. F. Basal and alar cells. G. Costa in cross section. I. Habit with sporophytes. J. Stem in cross section. Scale in mm: bar = 0.05 (D, G, H, K); bar = 0.06 (C, E, F); bar = 0.08 (J); bar = 0.5 (A, L); bar = 0.6 (B); bar = 1.96 (I). A, F, L from *Allen 12736A*; B, G, I, J from *Allen 13810*; all other figure parts from *Allen 12851*.

surfaces papillose throughout, dorsal trabeculae and median line thick, ventral trabeculae faint; endostome yellowish white, papillose throughout, basal membranes low, segments linear, not keeled, not or faintly perforate, cilia absent. Spores rounded, 14–22 µm, lightly papillose. Calyptrae mitrate, densely ciliate-fringed at base, naked, smooth or lightly roughened above, 1–2 mm long.

Illustrations. Bartram (1931, Pl. 3 2); Bartram (1949, Fig. 131 D–F); Welch (1966, Figs. 131–138); Sharp *et al.* (1994, Fig. 574); Churchill and Linares (1995, Fig. 56 g–m); Duarte Bello (1997, Pl. 226); Buck (1998, Pl. 1 7–10); Gradstein *et al.* (2001, Fig. 105 J–P); Buck (2003, Fig. 83). Figure 134.

Habitat. On upper twigs, small branches, trunks of trees or treelets, tree ferns, fence posts, occasionally epiphyllous or on rotting branches, usually in or fallen from canopy, rarely terrestrial; 700–3050 m.

Distribution in Central America. BELIZE. Toledo: *Allen 18656A* (MO). GUATEMALA. Alta Verapaz: *Sharp 2962a* (FH, NY); Baja Verapaz: *Sharp 5209* (NY); Quetzaltenango: *Standley 85089* (F, FH); Quiché: *Sharp 5292a* (NY). HONDURAS. Comayagua: *Allen 13810* (MO); Cortés: *Allen 14364* (MO); Francisco Morazán: *Standley 13350* (F); Lempira: *Allen 12008* (MO); Ocotepeque: *Allen 14424* (MO); Olancho: *Allen 12736A* (MO). COSTA RICA. Alajuela: *Crosby 3796* (MO); Cartago: *Crosby & Crosby 5947* (MO); Heredia: *Crosby & Crosby 8548* (MO); Puntarenas: *Gómez 25379* (MO); San José: *Crosby & Crosby 5895* (MO). PANAMA. Bocas del Toro: *Allen 5249* (MO); Coclé: *Crosby 4392B* (MO, PMA); Veraguas: *Crosby 10150A* (MO).

World range: Mexico; Central America; Caribbean; Western and Northern South America; Brazil.

Daltonia longifolia, one of the most common *Daltonia* species in Central America, is typically found on canopy twigs at high elevations. Many of the collections examined were made from fallen branches or the canopy branches of fallen trees. Its plants are relatively robust for *Daltonia* and have erect, mostly unbranched stems that usually grow as small, isolated patches. *Daltonia longifolia* has ovate-lanceolate leaves that are spirally twisted or contorted when dry, strongly keeled, and have plane margins with strongly developed borders. The upper and median leaf cells are oval-oblong to somewhat fusiform, thick-walled, and variably porose. Although the basal cells are longer, broader, and more consistently porose than the upper cells, there is a gradual transition between them, which gives the cells a more or less homogeneous aspect. Asexual propagula have not been reported before for *D. longifolia*, but they were observed in a single collection from Honduras (*Allen 12851*, MO). The propagula come from the base of costae on the abaxial side of the leaf. Sporophytically, *D. longifolia* has long setae that are scabrose above but smooth below and vary from 4–10 mm in length. Its erect, symmetric capsules are usually constricted at the neck and have strongly collenchymatous exothecial cells. The endostome is reduced, with a short basal membrane, linear segments, and no cilia. The calyptrae are mitrate and densely ciliate-fringed. Collections of *D. longifolia* commonly also contain plants of *D. stenophylla*, *D. gracilis*, or *D. tenuifolia.* As noted by Buck (1998), *D. longifolia* can best be recognized by its large size and leaves that are spirally contorted when dry.

Daltonia longifolia differs from all other Central American *Daltonia* species, except *D. pulvinata*, in having plane leaf margins. Bartram (1931) expressed "considerable mental reservation" about keeping *D. pulvinata* distinct from *D. longifolia.* However, *D. pulvinata* clearly differs from *D. longifolia* in having short, rhombic, non-porose upper leaf cells as well as abruptly enlarged and bulging, oblong to rectangular, non-porose basal cells. Attempts to distinguish the two species on the basis of margin stance, border width, setae form, and presence of or absence of propagula all fail to separate them.

5. *Daltonia peruviana* Mitt., J. Linn. Soc., Bot. 12: 401. 1869. Protologue. Andes Peruvianae, Cordillera de Raneo, Sachapata, *Lechler*. Types. Sachapata Cordillera Peruv., *Lechler* (NY, isotype); Cordillera of Peru, *Lechler* (NY, isotype).

Plants medium-sized, 1–3 cm tall, glossy, green to yellowish green. Stems erect, sparsely and irregularly branched, evenly foliate, dark red; stems in cross section with hyalodermis of enlarged, reddish cells, subepidermis of 1–3 rows of small, thick-walled, red cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 3–4 cells

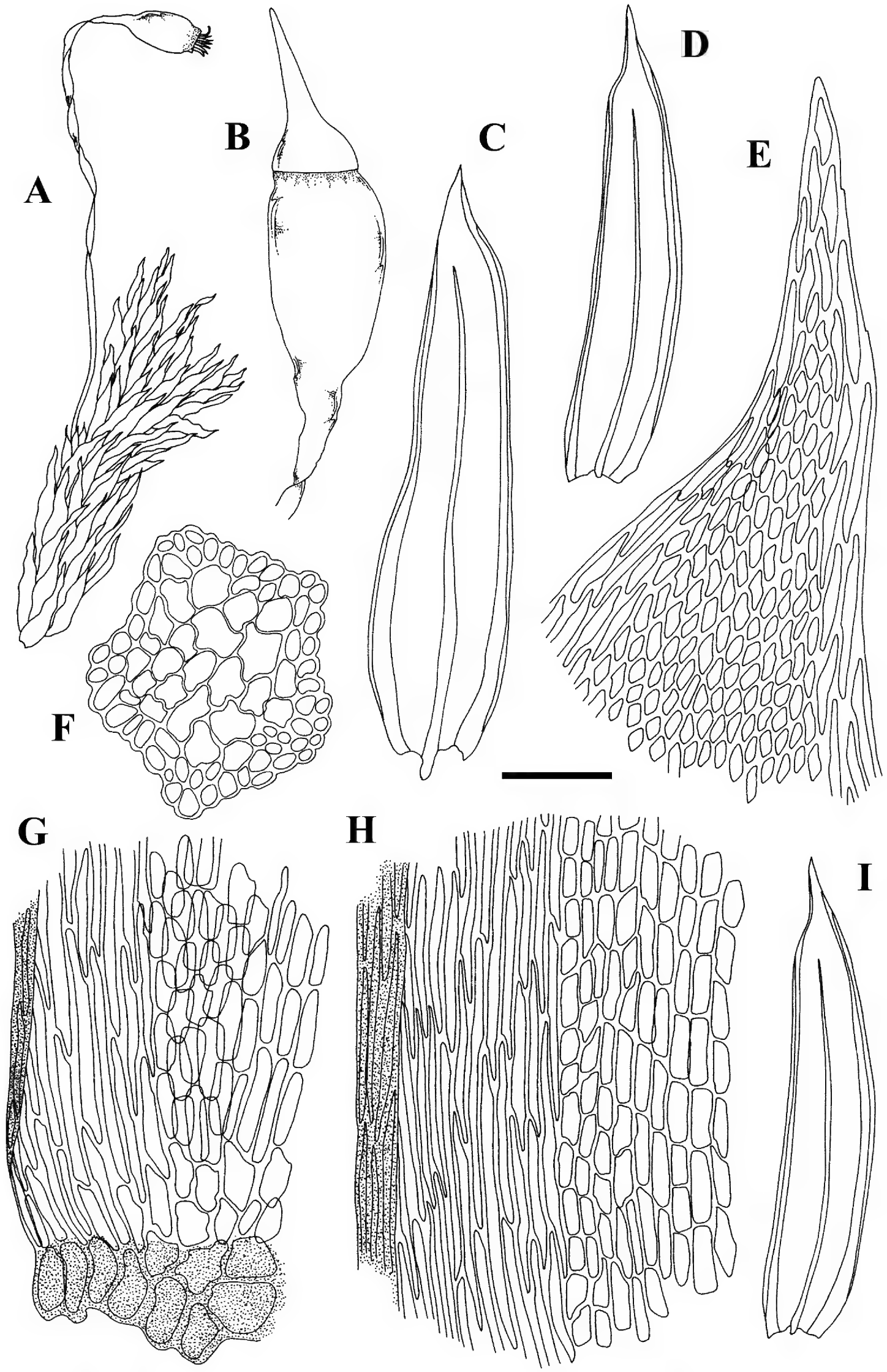
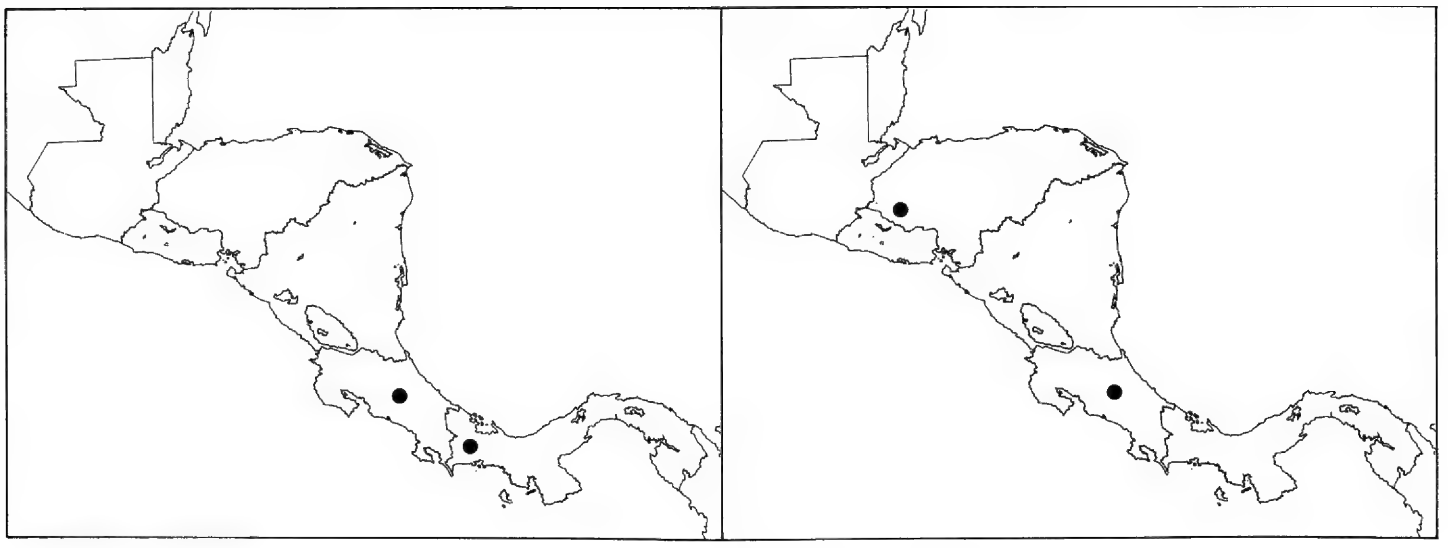


Figure 135. *Daltonia peruviana*. A. Habit with sporophyte. B. Seta, capsule, and operculum. C, D & I. Leaves. E. Leaf apex. F. Stem in cross section. G. Basal and alar cells. H. Upper basal leaf cells and margin. Scale in mm: bar = 0.06 (E, G, H); bar = 0.13 (F); bar = 0.6 (B–D, I); bar = 2.0 (A). B from *Crosby 13132A*; all other figure parts from *Allen 9062*.



Daltonia peruviana *Daltonia pulvinata*

long, basal 1–2 cells short-rectangular, reddish brown, upper cells oblong-elongate, hyaline; rhizoids at base of stems, around branch primordia, and at times along the stems, smooth, reddish brown, initials abaxial to the leaf insertions and from scattered initials, at times pinnately branched. Leaves isophyllous, erect-flexuose, somewhat crispate when dry, erect when wet, oblong-lanceolate, 2.5–3.0 mm long, 0.5–0.8 mm wide at base, deeply keeled in lower 1/2, acuminate, decurrent; margins narrowly recurved, bordered by elongate cells, thick-walled, 10–15 cells wide below, entire throughout, rarely minutely denticulate near the apices; costae single, strong, often flexuose, ending 7/8 the leaf length, in cross section cells homogeneously thick-walled; upper cells oval-hexagonal, 12–24 × 4–8 µm, smooth, firm-walled, median cells similar but somewhat larger; basal cells oblong, rectangular, or subrectangular, thin-walled, firm or bulging, 30–60 × 8–16 µm, cells across the insertions enlarged, irregularly rectangular to subquadrate, reddish brown, porose. Asexual propagula not seen. Autoicous. Perichaetia lateral on stems. Setae elongate, 5–12 mm long, red, scabrose above, smooth below. Capsules erect, ovoid to oblong, more or less constricted at the neck, symmetric, 1–2 mm long; exothecial cells at the mouth oblate in 3–4 rows, lower cells larger, oblate, rounded-quadrate, or subrectangular, collenchymatous; stomata on neck; opercula conic-rostrate, 1.0 mm long; annuli rudimentary, persistent; peristome diplolepideous; exostome teeth reddish yellow at base, recurved when wet, incurved when dry, narrowly triangular, both surfaces papillose throughout, dorsal trabeculae and median line thick, ventral trabeculae faint; endostome yellowish white, spiculose-papillose above, basal membranes low, segments linear, not keeled, not or faintly perforate, cilia absent. Spores rounded, 20–30 µm, lightly papillose. Calyptrae mitrate, densely ciliate-fringed at base, naked, smooth or lightly roughened above, 1.0–1.5 mm long.

Illustrations. Bartram (1931, Pl. 4 13). Figure 135.

Habitat. On shrubs, trees, and twigs; 2200–3050 m.

Distribution in Central America. COSTA RICA. Cartago: *Crosby & Crosby* 8186 (MO). PANAMA. Chiriquí: *Allen 9062* (MO).

World range: Central America; Western South America.

Daltonia peruviana is a medium-sized species with erect, weakly branched stems. It has oblong-lanceolate leaves that are erect-flexuose to erect-crispate when dry, and this gives the plants an aspect not encountered in other Central American species of *Daltonia*. The leaves have tightly recurved margins and strongly developed borders that are 10–15 linear cells wide at the leaf base. The upper and median leaf cells are oval-hexagonal and firm-walled. In strong contrast to the upper and median cells, the basal cells are enlarged, oblong to variously rectangular, thin-walled, and often bulging. Sporophytically, *D. peruviana* has long setae that are scabrose above and vary from 5–12 mm in length. Its erect, symmetric capsules are usually constricted at the neck and have strongly collenchymatous exothecial cells. The calyptrae are mitrate and densely ciliate-fringed.

Daltonia longifolia is similar to *D. peruviana* in size, and it is the only other Central American species with such well-developed leaf borders. It differs from *D. peruviana* in having plane leaf margins and short basal leaf cells that grade more or less smoothly into the upper leaf cells. Although *D. trachyodonta*, *D. tenuifolia*, and *D. gracilis* come out in the key near *D. peruviana*, they differ considerably in their smaller, narrower leaves and more weakly developed leaf borders. Nevertheless, care should be taken when separating *D. trachyodonta* and *D. peruviana* because the leaves of these species are similar in shape, and they have a comparable areolation. In addition to its smaller size and weaker border, *D. trachyodonta* differs from *D. peruviana* in having leaves that are tightly, spirally twisted around the stems when dry.

6. *Daltonia pulvinata* Mitt., J. Linn. Soc., Bot. 12: 398. 1869. Protologue. [Colombia] Andes Bogotenses, prope Bogota, *Weir.* Type. Andes Bogotenses, *Weir* (NY, holotype).

Plants small to medium-sized, 1.0–1.5 cm tall, glossy, green to yellowish green. Stems erect, sparsely and irregularly branched, evenly foliate, dark red; stems in cross section with somewhat enlarged epidermis of 1–2 rows of firm-walled, red cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 3–4 cells long, basal 1–2 cells short-rectangular, reddish brown, upper cells oblong-elongate, hyaline; rhizoids at base and along stems, smooth, reddish brown, from initials at base of costae on abaxial side and from scattered initials, at times pinnately branched. Leaves isophyllous, spirally contorted when dry, erect-flexuose when wet, lanceolate to oblong-lanceolate, 2.5–3.2 mm long, often deeply keeled in lower 1/2, sharply acuminate, decurrent; margins plane throughout, or at times broadly reflexed on one side, bordered by elongate, thick-walled, sometimes porose cells, 6–10 cells wide at base, entire throughout or minutely denticulate near the apices; costae single, strong, often flexuose, ending 7/8 the leaf length, in cross section cells homogeneously thick-walled; upper cells rhombic, 10–14 × 6–10 µm, smooth, median cells similar, at times in oblique rows, basal leaf cells oblong to rectangular, enlarged and bulging, 30–60 × 8–12 µm; alar cells enlarged, irregularly rectangular to subquadrate, reddish brown, porose, cells across the insertions enlarged, reddish, porose. Asexual reproduction occasionally by multicellular, uniseriate, clavate to fusiform propagula, abaxial at the base of the costa. Autoicous. Perichaetia lateral on stems. Setae elongate, 5–8 mm long, red, scabrose above, smooth below. Capsules erect, ovoid, more or less constricted at the neck, symmetric, 1.0–1.5 mm long; exothecial cells at the mouth oblate in 3–4 rows, lower cells larger, oblate, rounded-quadrate, or subrectangular, collenchymatous; stomata on neck; opercula conic-rostrate, 0.3–0.5 mm long; annulus not seen; peristome diplolepideous; exostome teeth yellow, recurved when wet, incurved when dry, narrowly triangular, both surfaces papillose throughout, dorsal trabeculae and median line thick, ventral trabeculae faint; endostome yellowish white, papillose throughout, basal membranes low, segments linear, not keeled, not or faintly perforate, cilia absent. Spores rounded, 22–25 µm, lightly papillose. Calyptrae mitrate, densely ciliate-fringed at base, naked, smooth or lightly roughened above, 1–2 mm long.

Illustrations. Bartram (1931, Pl. 3 1); Welch (1974, Figs. 134–148); Sharp *et al.* (1994, Fig. 573). Figure 136.

Habitat. On trunks of small trees; 2300–3109 m.

Distribution in Central America. HONDURAS. Lempira: *Allen 11436C* (MO). COSTA RICA. Cartago: *Bowers 636-A* (NY, TENN).

World range: Mexico; Central America; Western and Northern South America.

Daltonia pulvinata is a relatively small species. Its erect plants have mostly unbranched stems. It has lanceolate to oblong-lanceolate, keeled leaves that are spirally twisted or contorted when dry. The leaf margins of *D. pulvinata* have well-developed borders and, although the margins can be broadly reflexed on one side, they are mostly plane. The upper and median leaf cells are rhombic, firm-walled, and not porose. The basal cells are oblong to rectangular, enlarged, bulging, thin- to firm-walled, and more or less abruptly differentiated from the upper cells. Asexual propagula often occur in collections of *D. pulvinata*. The propagula come from the base of costae on the abaxial side of the leaf in the same region that rhizoidal initials are found. Sporophytically, *D. pulvinata* has long setae that are scabrose

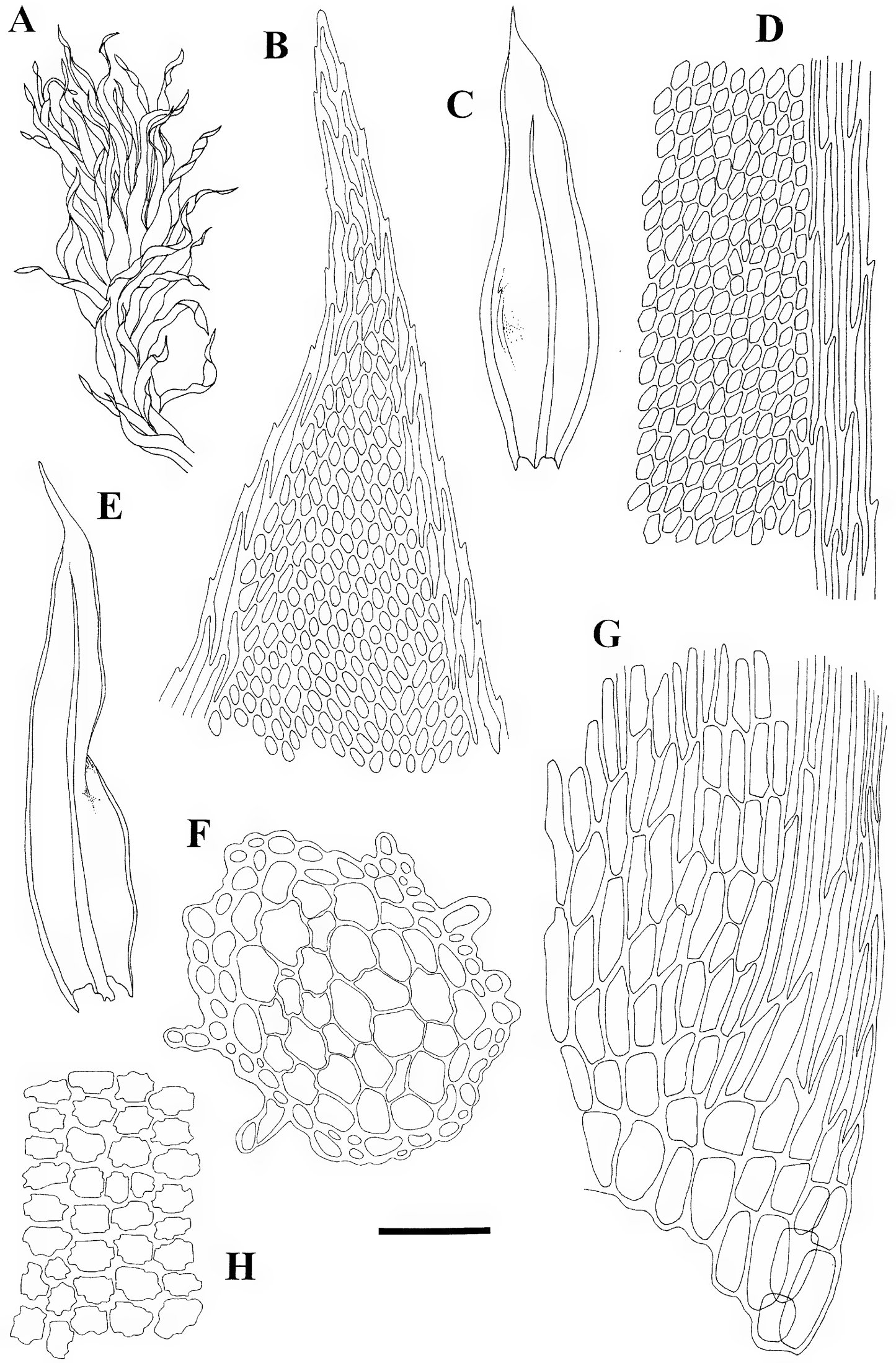


Figure 136. *Daltonia pulvinata*. A. Habit. B. Leaf apex. C & E. Leaves. D. Median leaf cells and margin. F. Stem in cross section. G. Basal and alar cells. H. Exothecial cells. Scale in mm: bar = 0.06 (B, D, G); bar = 0.08 (F, H); bar = 0.71 (C, E); bar = 1.56 (A). All figure parts from *Sharp 4624b*.

above but smooth below. Its erect, symmetric, ovate capsules are usually constricted at the neck and have strongly collenchymatous exothecial cells. The endostome is reduced, with low basal membranes, linear segments, and no cilia. The calyptrae are mitrate and densely ciliate-fringed.

Daltonia pulvinata differs from all other Central American *Daltonia* species, except *D. longifolia*, in having plane leaf margins. Bartram (1931) questioned whether *D. pulvinata* was distinct from *D. longifolia*. However, the presence of longer, often fusiform and porose upper leaf cells as well as the occurrence of short, firm-walled basal cells in *D. longifolia* adequately separates them. Previous attempts to distinguish the two species on the basis of margin stance, border width, seta form, and presence of or absence of propagula failed to separate them.

7. *Daltonia stenophylla* Mitt., J. Linn. Soc., Bot. 12: 402. 1869. Protologue. [Ecuador] Andes Quitenses, in montibus Tunguragua (8000 ped.), *Spruce, n. 568*; Llalla (9000 ped.), *Spruce, n. 567*. Types. Tunguragua, *Spruce 568* (NY, syntype); Lalla, *Spruce 567* (NY, syntype).

Daltonia aristifolia E. B. Bartram, Contr. U.S. Natl. Herb. 26: 99. 1928, illegitimate homonym, not *Daltonia aristifolia* Renauld & Cardot, 1896. Protologue. Costa Rica. Southern slope of Volcán de Turrialba, Costa Rica, altitude 2000 to 2400 meters, *Paul C. Standley*, February 22, 1924, *no. 35156a*. Types. Southern slope of Volcán de Turrialba, near the Finca del Volcán Turrialba, alt. 2000–2400 meters, on tree, Feb. 22, 1924, *Paul C. Standley No. 35156a* (US, holotype; FH, isotype).

Plants small, 0.3–1.5 cm tall, glossy, green to yellowish green. Stems erect, sparsely and irregularly branched, evenly foliate, dark red; stems in cross section with 1–2 rows of enlarged, reddish hyalodermis cells sometimes with a central pore, subepidermis of 1–2 rows of small, firm- to thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 3–4 cells long, basal 1–2 cells short-rectangular, reddish brown, upper cells oblong-elongate, hyaline; rhizoids at base of stems, around branch primordia, and along the stems, smooth, reddish brown, from scattered initials, weakly branched, branches with transverse cross walls. Leaves isophyllous, erect, flexuose-twisted when dry, erect to erect-spreading, somewhat flexuose when wet, lanceolate to linear-lanceolate, 2–3 mm long, keeled in lower 1/2, narrowly acuminate, decurrent; margins narrowly revolute on one or both sides, at times plane, the extreme base bordered by elongate, thick-walled, sometimes porose cells, (4–)5–8 cells wide, entire; costae single, strong, often flexuose, ending 3/4–7/8 the leaf length, in cross section cells homogeneously thick-walled; upper cells narrowly rhomboidal to long-fusiform, 30–50 × 5–7 µm, often porose, smooth, median cells at times a little longer, otherwise similar; basal cells linear, firm-walled, tapered at ends, often porose, somewhat wider than the linear border cells but otherwise identical, 30–60 × 4 µm; alar cells not differentiated, cells across the insertions enlarged and reddish. Asexual reproduction occasionally by multicellular, uniseriate, clavate to fusiform propagula, abaxial at the base of the costa. Autoicous or synoicous. Perichaetia lateral on stems. Setae elongate, 4–9 mm long, red, scabrose above, smooth below. Capsules erect or slightly inclined, ovoid to oblong, more or less constricted at the neck, symmetric, 1.0–1.2 mm long; exothecial cells at the mouth oblate in 3–4 rows, lower cells larger, oblate, rounded-quadrate, or subrectangular, collenchymatous; stomata on neck; opercula conic-rostrate, 0.7 mm long; annuli rudimentary, persistent; peristome diplolepideous; exostome teeth yellow, recurved when wet, incurved when dry, linear-triangular, both surfaces papillose throughout, dorsal trabeculae and median line thick, ventral trabeculae faint; endostome yellowish white, papillose throughout, basal membranes low, segments linear, not keeled, not or faintly perforate, cilia absent or rudimentary. Spores rounded, 10–20 µm, lightly papillose. Calyptrae mitrate, densely ciliate-fringed at base, naked, smooth or lightly roughened above, 0.7 mm long.

Illustrations. Bartram (1928a, Fig. 31, as *D. aristifolia*); Bartram (1931, Pl. 4 10); Welch (1971b, Figs. 104–113); Duarte Bello (1997, Pl. 227); Buck (1998, Pl. 1 1–6). Figure 137.

Habitat. On shrubs and twigs; 2000–2900 m.

Distribution in Central America. HONDURAS. Ocotepeque: *Allen 14424* (MO, filed under *D. longifolia*); Olancho: *Allen 12736* (MO). COSTA RICA. Cartago: *McAlpin BA-99* (MO); San José: *Richards R6171* (NY).

World range: Mexico; Central America; Caribbean; Western and Northern South America, Brazil.

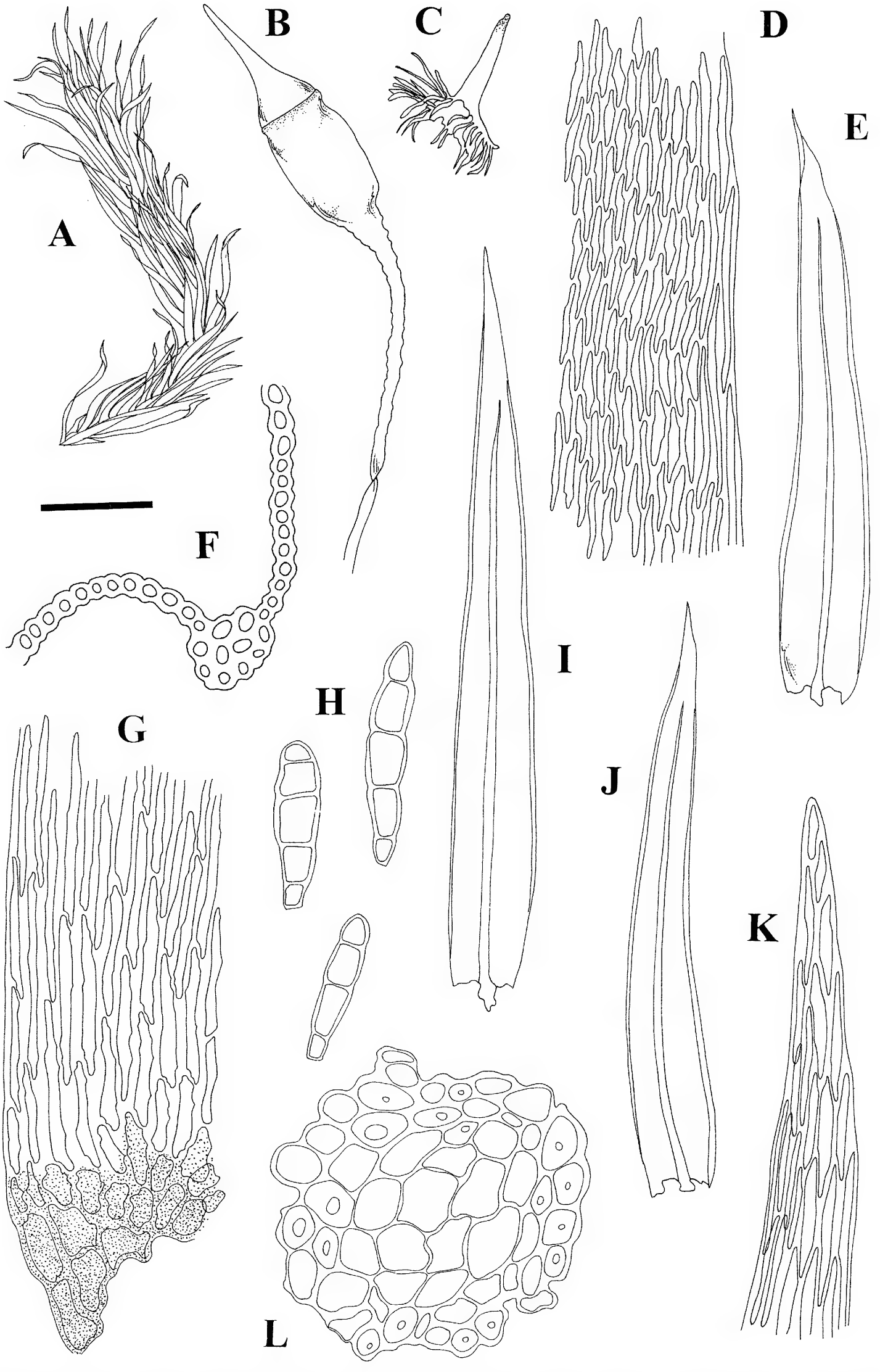
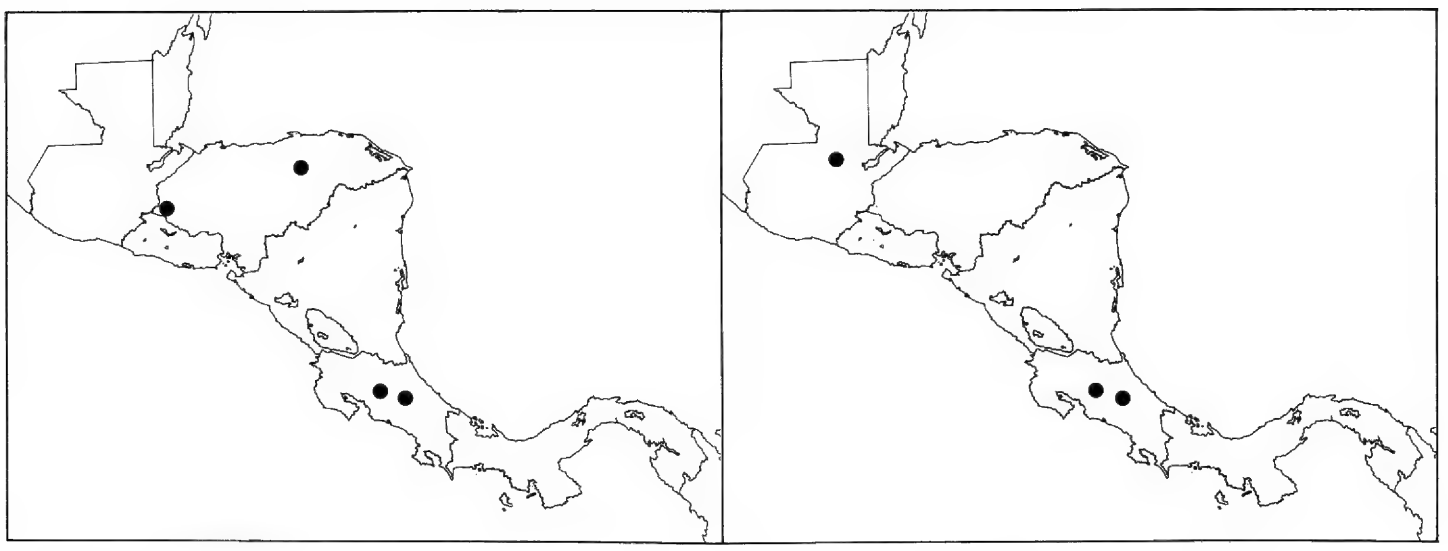


Figure 137. *Daltonia stenophylla*. A. Habit. B. Seta, capsule, and operculum. C. Calyptra. D. Median leaf cells and margin. E, I & J. Leaves. F. Costa in cross section. G. Basal and alar cells. H. Gemmae. K. Leaf apex. L. Stem in cross section. Scale in mm: bar = 0.05 (F); bar = 0.06 (D, G, H, K); bar = 0.08 (L); bar = 0.5 (B, C, E, I, J); bar = 1.96 (A). All figure parts from *Allen 12736*.



Daltonia stenophylla *Daltonia tenuifolia*

Daltonia stenophylla is a slender species with erect stems that, in Central America, grows in small, isolated patches. Its type collection is from Ecuador; it seems to be fairly common in the Caribbean, but it is rare in Central America. It has lanceolate to linear-lanceolate leaves that are 2–3 mm long, and typically erect to flexuose-twisted when dry. The leaves are narrowly acuminate and have marginal borders that are mostly 5–8 cells wide at the base. The upper and median leaf cells are narrowly rhomboidal to long-fusiform and often porose. The basal cells are linear, firm-walled, often porose, and taper at the ends. They are a little broader than the marginal border cells, but otherwise so similar it can be difficult to distinguish one from the other. As in most other species of *Daltonia*, asexual propagula often occur at base of costae on the abaxial side of the leaf. The setae of *D. stenophylla* are 4–7(–9) mm in length and scabrose above. Its erect, symmetric capsules have stomata at their constricted neck, and the exothecial cells are strongly collenchymatous.

Daltonia stenophylla belongs to the Central American *Daltonia* group that has lanceolate to linear-lanceolate, narrowly acuminate leaves with tightly revolute leaf margins. In Central America it can be confused with *D. gracilis* or *D. tenuifolia*, which are similar to *D. gracilis* in size, leaf stance, and leaf shape. *Daltonia gracilis* differs from *D. stenophylla* in having shorter upper leaf cells and oblong to rectangular basal leaf cells with more or less transverse end walls. Furthermore, the marginal border cells in *D. gracilis* are sharply and clearly demarcated from the basal leaf cells. *Daltonia tenuifolia* also has shorter upper leaf cells than *D. stenophylla* and further differs in having oblong, thin-walled, bulging basal leaf cells and smooth setae. In older material of *D. tenuifolia* the thin-walled basal cells collapse when dry and often fail to expand when re-hydrated.

8. *Daltonia tenuifolia* Mitt., J. Linn. Soc., Bot. 69: 402. 1869. Protologue. [Ecuador] Andes Quitenses, Pallatanga ad arbores (6000 ped.), *Spruce, n. 561*. Type. Pallatanga ad arbores, *Spruce 561* (NY, holotype).

Daltonia lorifolia Müll. Hal., Flora 58: 550. 1875. Protologue. Costa Rica, Candelaria, in foliis arborum inter Hepaticas cum *Meteorio Oerstediano*: *A. S. Oersted* leget et misit. Type. Costa Rica. Candelaria, in foliis arboreum inter Hepaticas, leg. *Oersted* (FH, isotype).

Plants small, 0.3–0.6 cm tall, glossy, green to yellowish green. Stems erect, sparsely and irregularly branched, evenly foliate, dark red; stems in cross section with 1–2 rows of enlarged, reddish hyalodermis cells, subepidermis of 1 row of small, firm- to thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2–4 cells long, basal 1–2 cells short-rectangular, reddish brown, upper 1–2 cells oblong-elongate, hyaline; rhizoids at base of stems, around branch primordia, and along the stems, smooth, reddish brown, from scattered initials, weakly branched, branches with transverse cross walls. Leaves isophyllous, erect, flexuose-twisted when dry, erect to erect-spreading, somewhat flexuose when wet, lanceolate to linear-lanceolate, 2.0–2.5 mm long, keeled in lower 1/2, narrowly acuminate, decurrent; margins narrowly revolute on one or both sides, sometimes plane at the extreme base, bordered by elongate, thick-

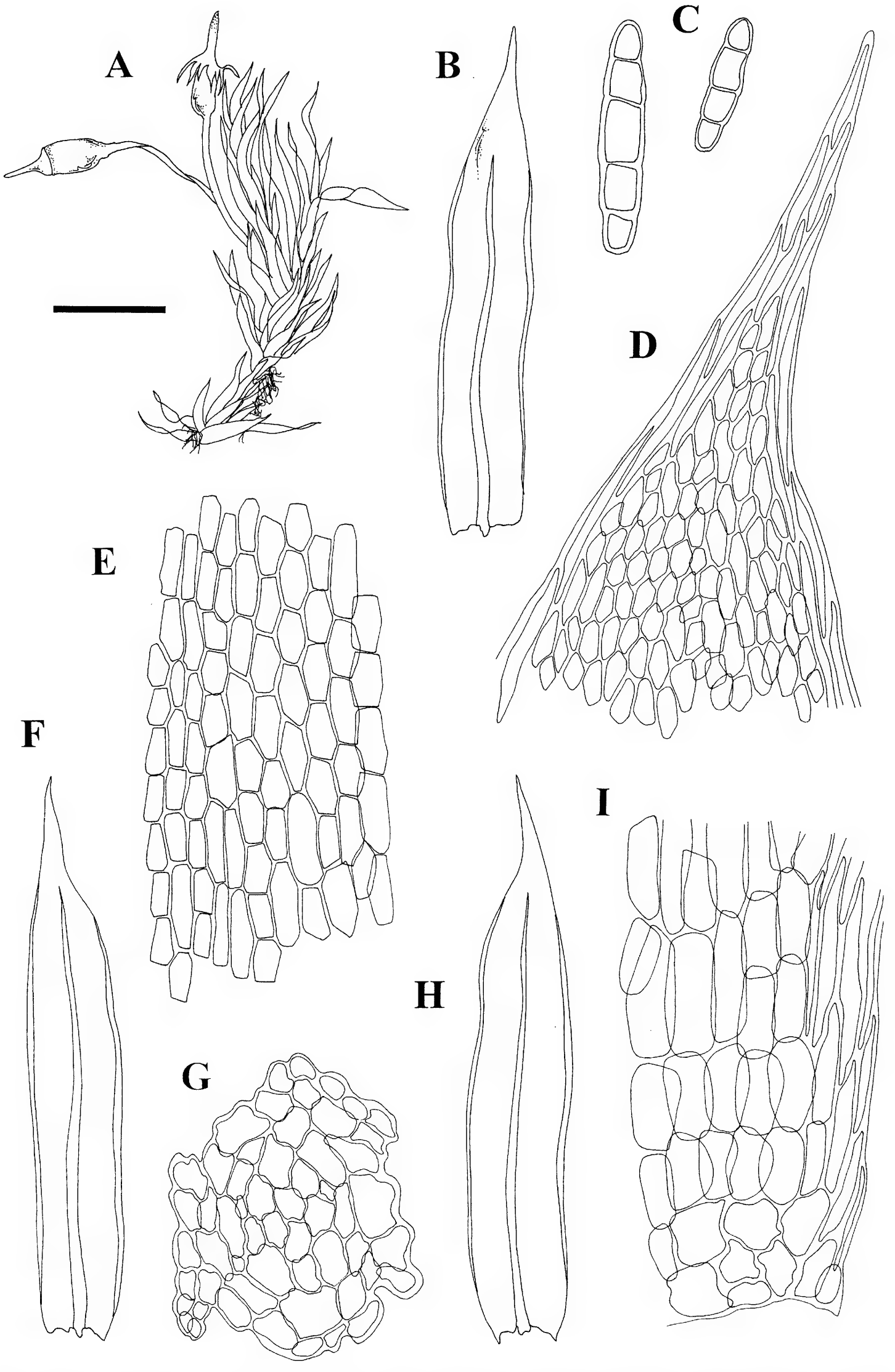


Figure 138. *Daltonia tenuifolia*. A. Habit with sporophytes. B, F & H. Leaves. C. Gemmae. D. Leaf apex. E. Median leaf cells. G. Stem in cross section. I. Basal and alar cells. Scale in mm: bar = 0.05 (C); bar = 0.06 (D, E, I); bar = 0.12 (G); bar = 0.5 (B, F, H); bar = 1.56 (A). All figure parts from *Valerio 205a*.

walled, sometimes porose cells, (2–)3–5 cells wide at base, entire; costae single, strong, often flexuose, ending 3/4–7/8 the leaf length, in cross section cells homogeneously thick-walled; upper cells subquadrate, oval-hexagonal, or rhombic, thin-walled, 14–32 × 6–14 µm, smooth, median cells longer, rhomboidal; basal cells oblong to long-rectangular, thin-walled, strongly bulging, 50–90 × 14–18 µm; alar cells not differentiated, cells across the insertions enlarged and reddish. Asexual reproduction occasionally by multicellular, uniseriate, clavate to fusiform propagula, abaxial at the base of the costa. Autoicous. Perichaetia lateral on stems. Setae elongate, 3 mm long, red, smooth throughout or lightly roughened just below the capsule. Capsules erect or slightly inclined, ovoid to oblong, more or less constricted at the neck, symmetric, 0.7–1.0 mm long; exothecial cells at the mouth oblate in 3–4 rows, lower cells larger, oblate, rounded-quadrate, or subrectangular, collenchymatous; stomata on neck; opercula conic-rostrate, 0.7–1.0 mm long; annuli rudimentary, persistent; peristome diplolepideous; exostome teeth yellow, recurved when wet, incurved when dry, linear-triangular, both surfaces papillose throughout, dorsal trabeculae and median line thick, ventral trabeculae faint; endostome yellowish white, papillose throughout, basal membranes low, segments linear, not keeled, not or faintly perforate, sometimes united at tips, cilia absent or rudimentary. Spores rounded, 10–14 µm, smooth to lightly papillose. Calyptrae mitrate, densely ciliate-fringed at base, naked, smooth or lightly roughened above, 1–1.3 mm long.

Illustrations. Bartram (1931, Pl. 4 16); Bartram (1949, Fig. 131 G & H); Welch (1974, Figs. 149–159); Sharp *et al.* (1994, Fig. 575). Figure 138.

Habitat. On trees and shrubs; 1135–3170 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: *Sharp 2962A p.p.* (FH, filed with *D. longifolia*). COSTA RICA. Cartago: *Oersted* (FH); San José: *Valerio 205a* (FH, NY).

World range: Mexico; Central America; Western and Northern South America.

Daltonia tenuifolia is a small, slender species with leaves that are erect to flexuose-twisted and sometimes lightly spirally twisted when dry. Its lanceolate to linear-lanceolate leaves are narrowly acuminate and less than 2.5 mm long. The leaves are more weakly bordered than most other *Daltonia* species, with the borders sometimes only three cells wide at base. The margins are narrowly revolute throughout. The upper leaf cells in *D. tenuifolia* are subquadrate, oval-hexagonal, or rhombic, and thin-walled. The basal cells are enlarged, bulging, thin-walled, and oblong to long-rectangular. Asexual propagula occur at the base of costae on the abaxial side of the leaf. Central American material of *D. tenuifolia* has setae only 3 mm long; however, in the type specimen they are 5–7 mm long. The setae in the type specimen are smooth to slightly roughened below the capsule, but in Central America the setae are often lightly roughened just below the capsule neck. Its erect, symmetric capsules have numerous stomata at their constricted neck, and the exothecial cells are strongly collenchymatous.

Daltonia tenuifolia belongs to the Central American *Daltonia* group with tightly revolute leaf margins. Within that group, it is similar to *D. stenophylla*, *D. gracilis*, and *D. trachyodonta* in plant size and leaf stance. *Daltonia stenophylla* and *D. gracilis* are also similar to *D. tenuifolia* in having linear-lanceolate to lanceolate leaves. *Daltonia stenophylla* differs from *D. tenuifolia* in having firm-walled, linear basal leaf cells that are often tapered at the ends. Furthermore, the basal leaf cells grade more or less smoothly into the marginal cells, making it hard to distinguish the basal cells from the marginal cells. *Daltonia gracilis* differs from *D. tenuifolia* in having firm-walled, not or weakly bulging basal leaf cells and setae that are scabrose above. *Daltonia trachyodonta* sometimes has bulging basal cells, but it differs from *D. tenuifolia* in having oblong-ligulate leaves that are strongly spirally twisted around the stem when dry, and short-oblong to subrectangular basal leaf cells.

9. *Daltonia trachyodonta* Mitt., J. Linn. Soc., Bot. 12: 400. 1869. Protologue. [Ecuador] Andes Quitenses, Cayambe, una cum *D. ovali Jameson*.

Daltonia trachydontia Mitt. *ex* E. B. Bartram, Bull. Torrey Bot. Club 58: 43. 1931, orthographic error.

Plants small, 0.3–1.0 cm tall, glossy, green to yellowish green. Stems erect, sparsely and irregularly branched, evenly foliate, dark red; stems in cross section with 1–2 rows of enlarged, reddish,

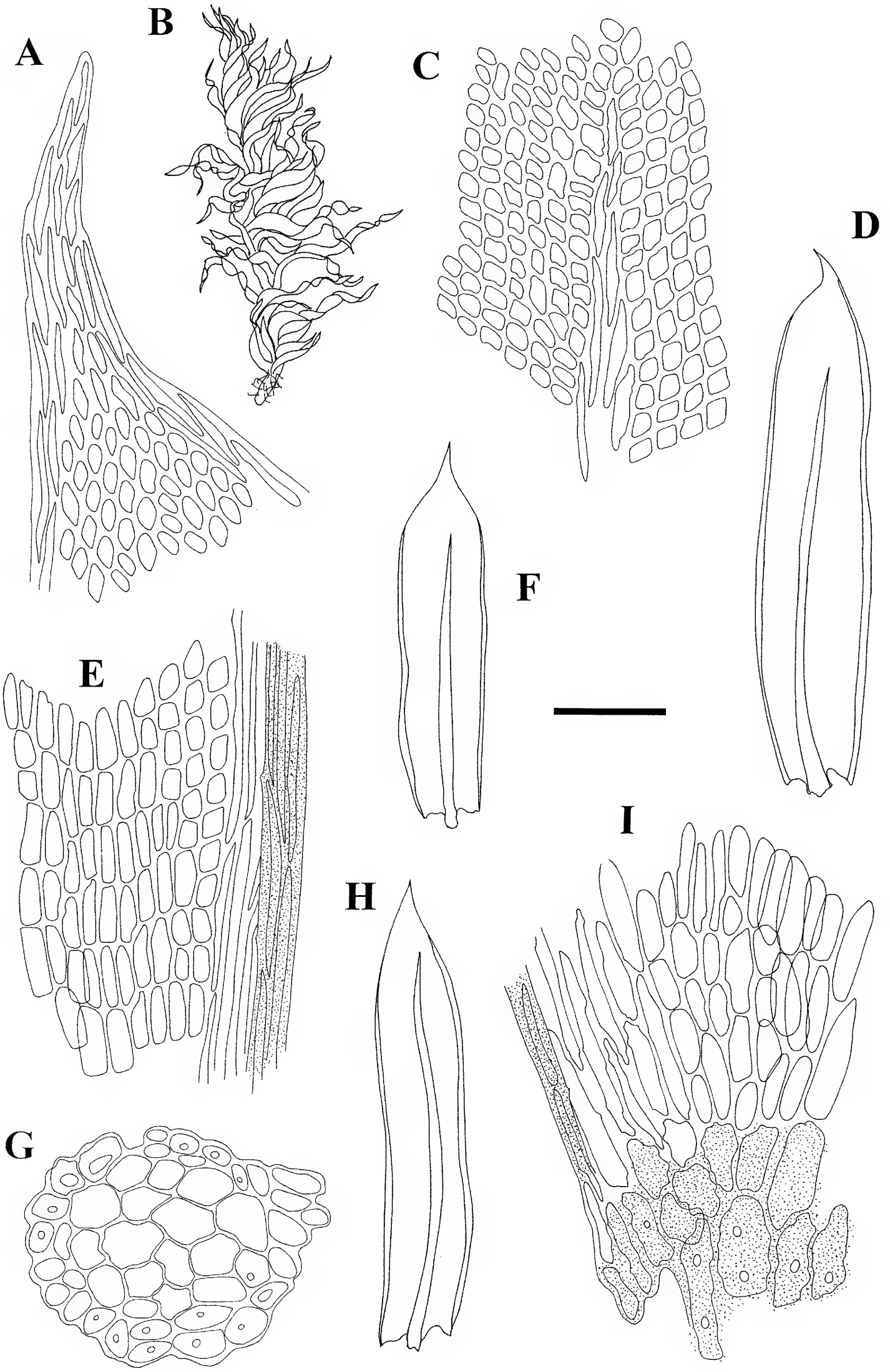
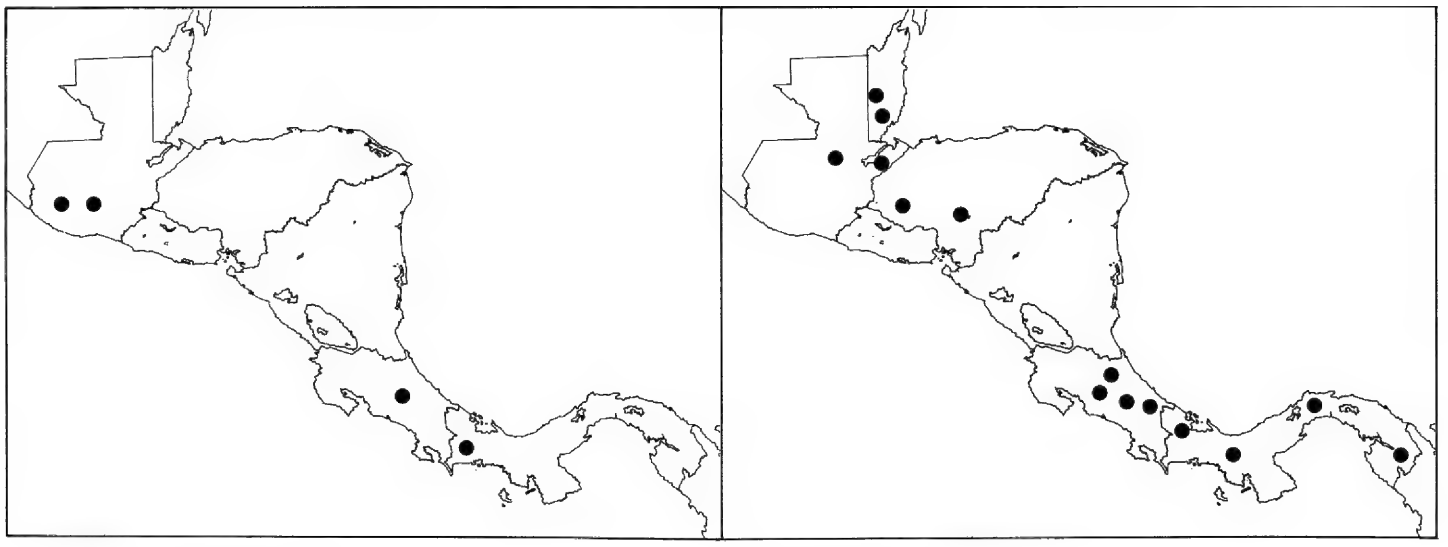


Figure 139. *Daltonia trachyodonta*. A. Leaf apex. B. Habit. C. Upper leaf cells and upper part of costa. D, F & H. Leaves. E. Median leaf cells and margin. G. Stem in cross section. I. Basal and alar cells. Scale in mm: bar = 0.06 (A, C, E, I); bar = 0.08 (G); bar = 0.5 (D, F, H); bar = 1.3 (B). All figure parts from *Allen 9062A*.



Daltonia trachyodonta *Leskeodon andicola*

often perforate hyalodermis cells, subepidermis of 1 row of small, firm- to thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2–4 cells long, basal 1–2 cells short-rectangular, reddish brown, upper 1–2 cells oblong-elongate, hyaline; rhizoids at base of stems, around branch primordia, and along the stems, smooth, reddish brown, from scattered initials, weakly branched, branches with transverse cross walls. Leaves isophyllous, erect, spirally twisted when dry, erect to erect-spreading, somewhat flexuose when wet, oblong-ligulate, 2.0–2.5 mm long, keeled in lower 1/2, acuminate, decurrent; margins narrowly revolute on one or both sides, sometimes plane at the base, bordered by elongate, thick-walled cells, 3–5 cells wide at base, entire; costae single, strong, often flexuose, ending 3/4–7/8 the leaf length, in cross section cells homogeneously thick-walled; upper cells oval-hexagonal, firm-walled, 14–18 × 8–10 µm, smooth, median cells longer, rhomboidal; basal cells oblong to rectangular, firm- to thin-walled, sometimes bulging, 50–90 × 14–18 µm; alar cells not differentiated, cells across the insertions enlarged and reddish. Asexual propagula not seen. Sporophytes not seen in Central America, description from Bartram (1931). Autoicous. Setae elongate, to 10 mm long, red, smooth throughout or lightly roughened below the capsule. Capsules erect, oval, to 1.5 mm long; opercula rostrate, erect, 0.75 mm long. Spores roughened, 12–16 µm in diameter. Calyptrae smooth above.

Illustrations. Bartram (1931, Pl. 4 15). Figure 139.

Habitat. On trees, branches, twigs, bamboo nodes, and *Guadua* sheaths; 750–3050 m.

Distribution in Central America. GUATEMALA. Sacatepéquez: *Standley 88961e* (F, FH); Suchitepéquez: *Standley 66941a* (F, filed with *D. gracilis*). COSTA RICA. Cartago: *Crosby 13134A* (MO). PANAMA. Chiriquí: *Allen 9062A* (MO).

World range: Central America; Western and Southern South America.

Daltonia trachyodonta is a small, slender species with leaves that are stiffly spirally twisted when dry. It has short, oblong-ligulate leaves that are less than 2.5 mm long. The leaves are weakly bordered, with borders sometimes only 3–5 cells wide at base. The upper leaf cells are oval-hexagonal and firm-walled and the basal cells are larger, oblong to rectangular, firm- to thin-walled, and occasionally bulging.

Daltonia trachyodonta belongs to a group of small Central American *Daltonia* species (*D. stenophylla*, *D. gracilis*, *D. tenuifolia*) with tightly revolute leaf margins. *Daltonia gracilis* and *D. tenuifolia* are also similar to *D. trachyodonta* in having oblong basal leaf cells. All these species differ from *D. trachyodonta* in having linear-lanceolate or lanceolate rather than oblong-ligulate leaves. *Daltonia stenophylla* further differs from *D. trachyodonta* in having linear basal leaf cells. The basal leaf cells in *D. tenuifolia* differ from those of *D. trachyodonta* in being thin-walled and bulging throughout. *Daltonia gracilis* also differs from *D. trachyodonta* in having leaves that are flexuose-twisted rather than spirally twisted when dry.

4. *Leskeodon* Broth., Nat. Pflanzenfam. I(3): 925. 1907.

Plants small or medium-sized, glossy, green, yellowish green, or reddish yellow, in tufts or thin to dense mats. Stems erect, sparsely and irregularly branched, somewhat complanate-foliate, dark red; stems in cross section with small, thin- or thick-walled epidermal cells, enlarged, thin-walled cortical cells, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 3–6 cells long, basal cell short-rectangular, reddish brown, upper cells oblong-elongate, hyaline; rhizoids at base of stems, around branch primordia, and on stems abaxial to the leaf insertions, smooth or papillose, reddish brown, at times pinnately branched. Lateral leaves wide-spreading, ventral and dorsal leaves smaller, erect-spreading when wet, all leaves somewhat contorted with undulate margins or curled-contorted to spirally twisted when dry, orbicular, ovate, obovate, oblong-ovate, oblong, or spathulate; acute to broadly rounded, mucronate, apiculate, cuspidate, or piliferous, apices often twisted, decurrent; margins entire, bordered by several rows of elongate cells, plane; costae single, slender, ending 1/2–3/4 the leaf length, in cross section cells homogeneously thick-walled; upper cells rounded, rhombic, hexagonal, or rhomboidal, smooth or porose, thin- or firm-walled, occasionally collenchymatous; basal cells oblong or fusiform-elongate, thin- or thick-walled, at times porose, juxtacostal basal cells sometimes differentiated, cells across the insertions enlarged, irregularly rectangular to subquadrate, reddish brown. Asexual reproduction by rhizoidal propagula or caducous leaves. Autoicous, synoicous, or dioicous. Perichaetia and perigonia lateral on stems. Setae elongate, smooth or roughened above. Capsules erect, ovoid, short-cylindric, or cylindric, constricted at the neck; exothecial cells sometimes collenchymatous; stomata on neck; opercula conic-rostrate; annuli rudimentary, persistent; peristome diplolepideous; exostome teeth yellow to whitish (sometimes reddish yellow), erect-recurved when wet, erect-incurved when dry, narrowly triangular, papillose throughout or faintly papillose to smooth; endostome yellowish white, papillose above, basal membranes low, segments linear, weakly keeled, not perforate, cilia rudimentary or absent. Calyptrae mitrate, sometimes with a few thick, ascending hairs, fimbriate at base.

Leskeodon is a genus of 18 species found in the tropical regions of the New World and Asia. It is primarily an epiphytic genus, but some of its species also grow along streams on rocks and boulders. Plants of *Leskeodon* are glossy, green, yellowish green, or reddish yellow, and have erect, sparsely branched stems. Its leaves are more or less complanate, vary from orbicular to ovate or oblong, and often have wavy margins. The stems and branches are dark red, lack central strands, and have naked branch buds. The rhizoids at times are densely pinnately branched, with secondary branches that have right-angled cross walls. The leaves of *Leskeodon* have weak, single costae, well-developed borders of elongate, linear cells, short, smooth cells, and often twisted apices. Nearly all Central American species of *Leskeodon* reproduce asexually by means of rhizoidal propagula.

Most species of *Leskeodon* are autoicous or synoicous, and sporophytes are commonly encountered in the genus. The sporophytes of *Leskeodon* have elongate setae, short-rostrate opercula, and ovoid, oblong, or short-cylindric capsules that sometimes have collenchymatous exothecial cells. *Leskeodon* has a diplolepideous peristome with usually yellowish or white exostome teeth that are papillose throughout on both surfaces. The teeth are hygrocastique: recurved when wet, erect or incurved when dry. They have reduced endostomes with low basal membranes, often broad, weakly keeled segments, and reduced or absent cilia. The calyptrae are mitrate and fimbriate at base.

Daltonia is the genus most likely to be confused with *Leskeodon* in Central America. Both genera have erect, weakly branched, deep red stems with unicostate leaves that lack alar cell development and are strongly bordered. They also have very similar sporophytes and fimbriate-fringed calyptrae. *Daltonia* differs from *Leskeodon* in having isophyllous leaves that are typically linear-lanceolate to ovate-lanceolate and deeply carinate at base. In addition, their leaf cells are usually longer and narrower than the mostly rounded to hexagonal or subhexagonal-rhomboidal cells of *Leskeodon*. Lastly, the leaf borders of *Daltonia* are usually much broader at base (sometimes 15 cells wide) than those of *Leskeodon*, and they tend to be narrower above, unlike those of *Leskeodon*, which are more or less uniform throughout the leaf.

Leskeodon is gametophytically almost identical to *Distichophyllum*, a genus centered in tropical Asia and Oceania but also found in temperate South America and Africa. The two genera differ in the ornamentation of their exostome teeth: *Distichophyllum* densely cross-striate on the dorsal surface,

with strong median furrows; *Leskeodon* papillose on the dorsal surface, median furrow absent. *Distichophyllidium*, a genus of five species found in Africa, Southeast Asia, and New Caledonia, has sporophytes identical to those of *Leskeodon* and their gametophytes are also very similar. It differs from *Leskeodon* only in having leaves that are strongly carinate at base (a feature present in *Daltonia*) and short, single or absent costae.

The name *Leskeodon* combines the generic name *Leskea* with the Greek *odon* (tooth) and apparently refers to the similarity of their peristome teeth. *Leskea* and *Leskeodon* have narrow, whitish, papillose exostome teeth and reduced endostomes. In *Leskea*, however, the exostome teeth are also often faintly cross-striate at base.

1. Basal leaf cells fusiform, thick-walled, usually porose; rhizoids papillose, densely branched; setae 6–10 mm long; capsules cylindric, cells collenchymatous in upper 1/3; exostome teeth smooth; spores 20–28 µm . . . . . 5. *L. palmarum*
1. Basal cells oblong, firm- or thin-walled, not porose; rhizoids usually smooth, weakly or densely branched; setae 2–6 mm long; capsules oblong to subcylindric, cells collenchymatous in upper 2/3; exostome teeth densely papillose; spores 8–16 µm (sporophytes unknown in *L. paisa*) 2

2. Upper leaf cells 16–22 µm long, thin-walled 3
2. Upper leaf cells 10–14 µm long, firm-walled 4

3. Leaves orbicular; upper cells not collenchymatous; apices apiculate . . . . . 4. *L. paisa*
3. Leaves obovate, oblong-obovate, or spathulate; upper cells collenchymatous; apices apiculate, cuspidate, or piliferous . . . . . 3. *L. cubensis*

4. Basal leaf cells thin-walled and bulging; juxtacostal basal cells abruptly enlarged, considerably larger than the outer basal cells . . . . . 1. *L. andicola*
4. Basal leaf cells firm-walled, not or slightly bulging; juxtacostal basal cells slightly larger than the outer basal cells . . . . . 2. *L. auratus*

1. *Leskeodon andicola* (Spruce *ex* Mitt.) Broth., Nat. Pflanzenfam. I(3): 926. 1907. *Distichophyllum andicola* Spruce *ex* Mitt., J. Linn. Soc., Bot. 12: 395. 1869. *Mniadelphus andicola* (Spruce *ex* Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 318. 1877. Protologue. Ins. Cuba, ad arbores, *Wright, n. 87* ex parte. Andes Quitenses, fl Bombonasa (1000–1500 ped.), *Spruce, n. 572*; in sylva Canelos (3000 ped.), *Spruce, n. 574*. Andes Peruvianae, in monte Campana juxta rivulum Sinchen (3000 ped.), *Spruce, n. 573*.

Leskeodon mexicanus Cardot, Rev. Bryol. 38: 41. 1911. Protologue. [Mexico] État de Vera-Cruz: Jalapa, Coatepec road, sur un tronc pourrissant de Fougère arborescente, associé à *Cyclodictyon albicans* (*Barnes et Land,* 1908, *n° 590 in parte*).

Plants small, 4–10 mm tall, glossy, yellowish green to dark green, in tufts or thin to dense mats. Stems erect, sparsely and irregularly branched, somewhat complanate-foliate, dark red; stems in cross section with hyalodermis of enlarged, reddish cells, subepidermis of 1–3 rows of small, thick-walled, red cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 3 cells long, basal cell short-rectangular, reddish brown, upper cells oblong-elongate, hyaline; rhizoids at base of stems, around branch primordia, and on stems abaxial to the leaf insertions, smooth, reddish brown, at times pinnately branched. Leaves erect, somewhat contorted with undulate margins when dry; lateral leaves wide-spreading when wet, ovate-oblong or ovate to spathulate, 1.5–2.5 mm long, ventral and dorsal leaves erect-spreading when wet, ovate to oblong-ovate, smaller than lateral leaves, 1.0–1.5 mm long, acute, mucronate, apiculate, or shortly cuspidate, decurrent; margins entire, bordered completely by 1–2 rows of elongate cells, sometimes border present below and weakly present or absent above midleaf, plane; costae single, slender, ending 1/2–3/4 the leaf length, in cross section cells homogeneously thick-walled; upper cells rounded, rhombic or hexagonal, 10–14 µm, smooth, firm-walled, occasionally somewhat collenchymatous, median cells similar but somewhat larger; basal cells enlarged, bulging, thin-walled, oblong, juxtacostal basal cells 30–46 µm long, cells across the insertions enlarged, irregularly rectangular to subquadrate, reddish

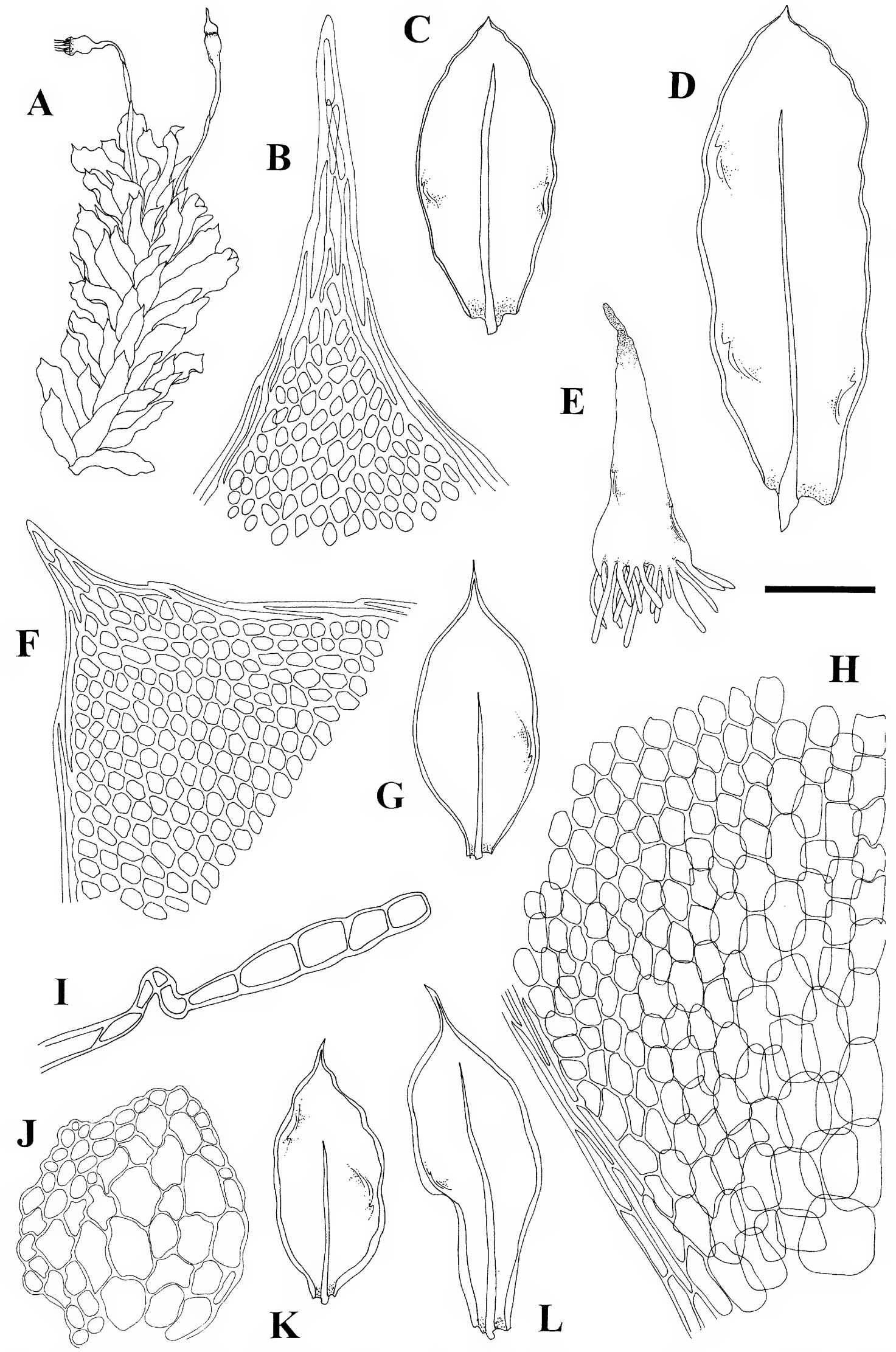


Figure 140. *Leskeodon andicola*. A. Habit with sporophytes. B & F. Leaf apices showing variation in single collection. C, G, K & L. Dorsal leaves. D. Lateral leaf. E. Calyptra. H. Basal and alar cells. I. Rhizoidal propagule. J. Stem in cross section. Scale in mm: bar = 0.05 (I); bar = 0.06 (B, F, H); bar = 0.13 (J); bar = 0.36 (E); bar = 0.5 (C, D, G, K, L); bar = 1.56 (A). K from *Standley 71632a*; L from *Crosby & Crosby 6345*; all other figure parts from *Allen 5550*.

brown. Asexual reproduction occasionally by rhizoidal propagula. Autoicous. Perichaetia and perigonia lateral on stems. Setae elongate, 3–6 mm long, red, roughened above, smooth below. Capsules erect, ovoid to short-cylindric, constricted at the neck, symmetric, 0.50–0.75 mm long; exothecial cells at the mouth short-rectangular, in 2–3 rows, lower cells larger, rounded-quadrate to subrectangular, thin-walled, weakly collenchymatous; stomata on neck; opercula conic-rostrate, 0.5 mm long; annuli rudimentary, persistent; peristome diplolepideous; exostome teeth reddish yellow, erect-recurved when wet, erect-incurved when dry, narrowly triangular, both surfaces papillose throughout, dorsal trabeculae and median line thick, ventral trabeculae faint; endostome yellowish white, spiculose-papillose above, basal membranes low, segments linear, weakly keeled, not perforate, cilia absent. Spores rounded, 8–12 µm, lightly papillose. Calyptrae mitrate, roughened-papillose above, fimbriate at base, 1 mm long.

Illustrations. Thériot (1940, Pl. 55 2); Bartram (1949, Fig. 132 A–D); Welch (1969, Figs. 208–213); Sharp *et al.* (1994, Fig. 578 a–f, h–j, as *L. mexicanus*); Churchill and Linares (1995, Fig. 57 a–d); Duarte Bello (1997, Pl. 234); Buck (1998, Pl. 3); Gradstein *et al.* (2001, Fig. 106 A–D). Figure 140.

Habitat. On treelet trunks, roots, twigs, leaves, rotting logs, and rocks near streams or rivers; 35–2600 m.

Distribution in Central America. BELIZE. Cayo: *Allen 15538* (MO); Toledo: *Whittemore 6494* (BRH, MO, NY). GUATEMALA. Alta Verapaz: *Standley 71632a* (F, FH); Izabal: *Steyermark 39075* (F, FH). HONDURAS. Francisco Morazán: *Allen 12378b* (MO); Lempira: *Allen 11912* (MO). COSTA RICA. Cartago: *Crosby & Crosby 5935* (CR, MO); Heredia: *Grayum 9991* (CR, MO); Limón: *Steere CR-137* (NY); San José: *Crosby & Crosby 5837* (MO). PANAMA. Bocas del Toro: *Allen 5550* (MO); Darién: *Folsom 6397* (MO); Panamá: *Crosby 4497B* (MO); Veraguas: *Crosby 10213* (MO).

World range: Mexico; Central America; Caribbean; Western and Northern South America.

Leskeodon andicola is a small species that grows as scattered tufts or mats. The plants have weakly crispate leaves with wavy margins when dry. There are two distinct forms of the species. The typical form has well-differentiated lateral and ventral/dorsal leaves. The lateral leaves are distinctly larger than the ventral and dorsal leaves and are mostly oblong. The leaf border in this form is fairly weak, sometimes absent above midleaf, and usually not fully merging at the mucronate apex. The second form, nomenclaturally centered on *L. mexicanus*, is a smaller, more slender plant than the typical form with weakly differentiated lateral and ventral/dorsal leaves. The leaves are ovate to spathulate, apiculate to cuspidate, and strongly bordered, with the border confluent at the apex.

All forms of the species have leaves with plane, entire margins and weak costae that end 1/2–3/4 the leaf length. The upper leaf cells are small, rounded to hexagonal, and firm-walled, while the basal cells are enlarged, bulging, and thin-walled. A distinctive feature of the species is the presence of greatly enlarged and bulging juxtacostal cells at the base of the leaf. Sporophytically, *L. andicola* has short setae that are lightly papillose below the capsules and ovoid to short-cylindric capsules with weakly collenchymatous exothecial cells.

Leskeodon auratus and *L. andicola* are very similar and likely to be confused. In aspect, plants of *L. auratus* have leaves more stiffly curled and contorted when dry than those of typical plants of *L. andicola*, which have crispate and wavy leaves when dry. The species have upper leaf cells identical in form and size. Furthermore, *L. auratus* and the *mexicanus*-form of *L. andicola* are similar in size, and their leaves are similar in stance and shape. *Leskeodon auratus* differs from *L. andicola* in having somewhat enlarged but firm basal leaf cells. Unfortunately, the basal leaf cells in *L. auratus* are variable and can sometimes be weakly bulging. The juxtacostal basal cells of *L. auratus*, however, are not enlarged and strongly differentiated as is typical for those of *L. andicola*. *Leskeodon cubensis* differs from *L. andicola* in having homogenous leaf cells and considerably larger upper leaf cells (16–30 µm long) that are thin-walled and usually collenchymatous. In addition, the most common form of *L. cubensis* has piliferous leaves.

The specific epithet *andicola* is a noun in apposition and has the same ending regardless of the gender of the generic name.

2. *Leskeodon auratus* (Müll. Hal.) Broth., Nat. Pflanzenfam. I(3): 926. 1907. *Mniadelphus auratus* Müll. Hal., Syn. Musc. Frond. 2: 26. 1851. *Distichophyllum auratum* (Müll. Hal.) Mitt., J. Linn. Soc., Bot. 12: 396. 1869. Protologue. Insula Antillarum Trinidad, ubi in monte Tocuche 4 Dec. 1847. legit *Crüger.*

Distichophyllum pusillum Mitt., J. Linn. Soc., Bot. 12: 394. 1869. *Mniadelphus pusillus* (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 318. 1877. *Leskeodon pusillus* (Mitt.) Broth., Nat. Pflanzenfam. I(3): 926. 1907. Protologue. [Colombia] Nova Granata, inter *Lophocoleam connatum* ad radicem filicis cujusdam, *Funck et Schlim.*

Plants small, 3–6(–10) mm tall, glossy, yellowish green to reddish yellow, in thin to dense mats. Stems erect, sparsely and irregularly branched, somewhat complanate-foliate, dark red; stems in cross section at times with enlarged, reddish hyalodermis cells, subepidermis of 1–2 rows of small, thick-walled, red cells, cortical cells enlarged, thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 3–4 cells long, 1–2 basal cells short-rectangular, reddish brown, upper 1–2 cells oblong-elongate, hyaline; rhizoids at base of stems, around branch primordia, and on stems abaxial to the leaf insertions, smooth or sometimes roughened, reddish brown, often pinnately branched. Leaves erect, curled-contorted when dry, lateral leaves wide-spreading when wet, ventral and dorsal leaves smaller than the lateral leaves, erect to erect-spreading when wet, ovate, obovate, oblong-ovate, oblong, or spathulate, 1–2 mm long, acute to broadly rounded, apiculate, or shortly cuspidate, apices at times twisted, decurrent; margins entire, bordered completely by 2–5 rows of elongate cells, plane; costae single, slender, ending 1/2–3/4 the leaf length, in cross section cells homogeneously thick-walled; upper cells rounded, rhombic, or hexagonal, 8–15 µm, smooth, firm-walled, median cells similar but somewhat larger; basal cells enlarged, firm-walled, occasionally somewhat bulging, oblong, juxtacostal basal cells longer, but not much broader, cells across the insertions enlarged, irregularly rectangular to subquadrate, reddish brown. Asexual reproduction occasionally by rhizoidal propagula. Autoicous, synoicous, or dioicous. Perichaetia and perigonia lateral on stems. Setae elongate, 4–6 mm long, red, roughened above, smooth below. Capsules erect, ovoid to short-cylindric, constricted at the neck, symmetric, 0.4–0.8 mm long; exothecial cells at the mouth short-rectangular, in 2–3 rows, lower cells in upper 2/3 of the capsule larger, rounded-quadrate, collenchymatous, cells in lower 1/3 short-rectangular, not collenchymatous; stomata on neck; opercula conic-rostrate, 0.5–0.7 mm long; annuli rudimentary, persistent; peristome diplolepideous; exostome teeth pale yellow to white, erect-recurved when wet, erect-incurved when dry, narrowly triangular, dorsal surface more thickly papillose than ventral surface, dorsal trabeculae and median line thick, ventral trabeculae faint; endostome yellowish white, papillose, basal membranes low, segments broad, faintly keeled, not perforate, cilia absent. Spores rounded, 12–16 µm, lightly papillose. Calyptrae mitrate, roughened-papillose above, fimbriate at base, 1 mm long.

Illustrations. Welch (1971b, Figs. 216–225); Welch (1972a, Figs. 250–260); Buck (1998, Pl. 2 5–9). Figure 141.

Habitat. On treelet stems, twigs, vines, leaves, roots, and rotting logs, occasionally on stream banks; 850–2550 m.

Distribution in Central America. BELIZE. Toledo: *Allen 15351* (MO). HONDURAS. Lempira: *Allen 11532* (MO, TEFH). COSTA RICA. Cartago: *Crosby & Crosby 5920* (MO); Heredia: *Crosby & Crosby 6053* (MO); San José: *Holz 359* (NY). PANAMA. Bocas del Toro: *Allen 5659* (MO); Panamá: *Crosby 10044* (MO).

World range: Central America; Caribbean; Western South America, Brazil.

Leskeodon auratus is a small species that often grows in dense mats. The plants are usually yellowish red, and the leaves, which are extremely variable in shape, are stiffly erect-curled and contorted when dry. The leaf apices are apiculate to shortly cuspidate, and the plane margins are strongly bordered. The upper leaf cells of *L. auratus* are small, rounded to hexagonal, and firm-walled, while the basal cells are oblong, enlarged, but firm-walled. Sporophytically, *L. auratus* has long setae that are lightly papillose below the capsules, and ovoid to short-cylindric capsules with collenchymatous exothecial cells in the upper two-thirds of the capsule.

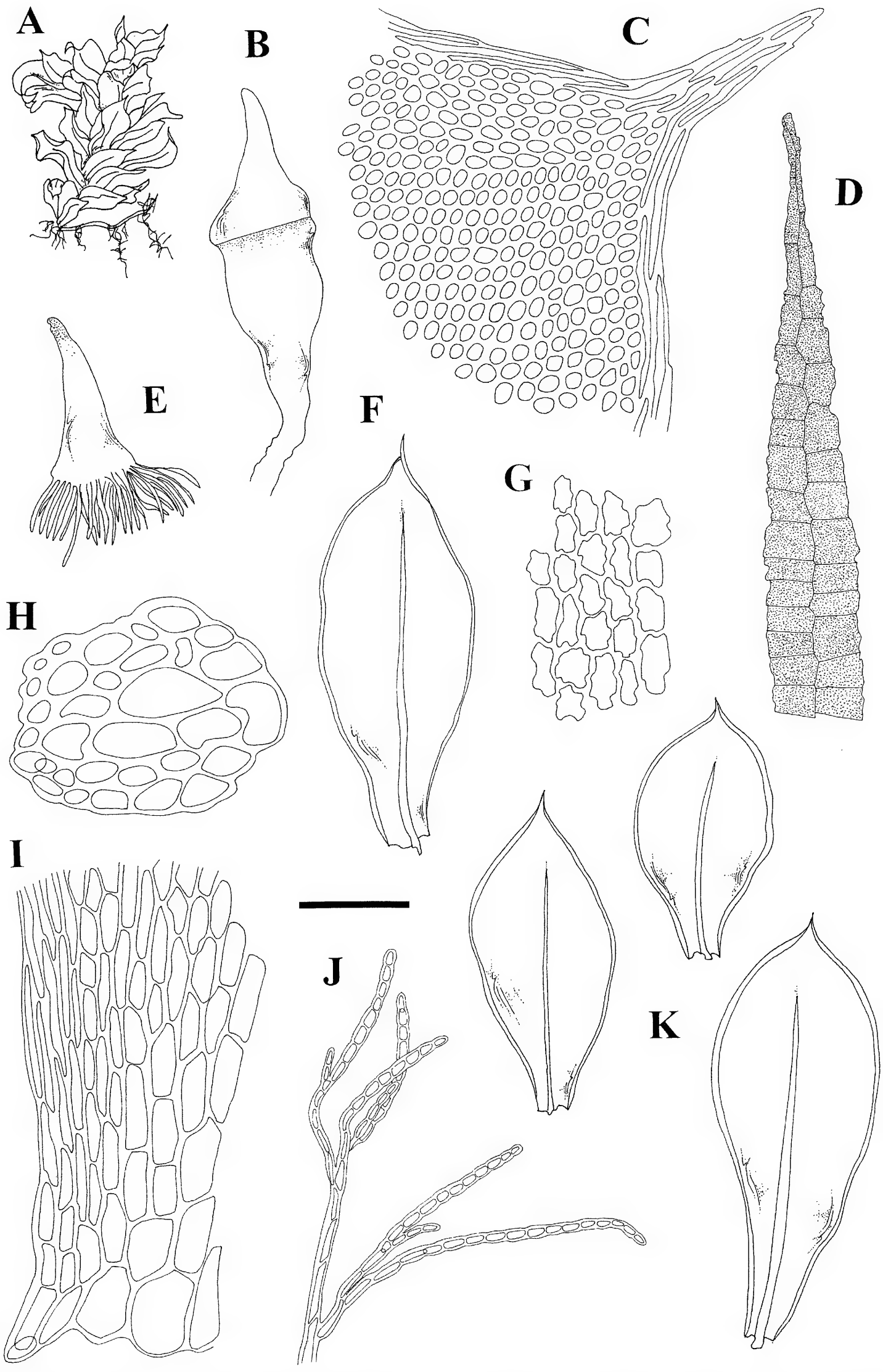
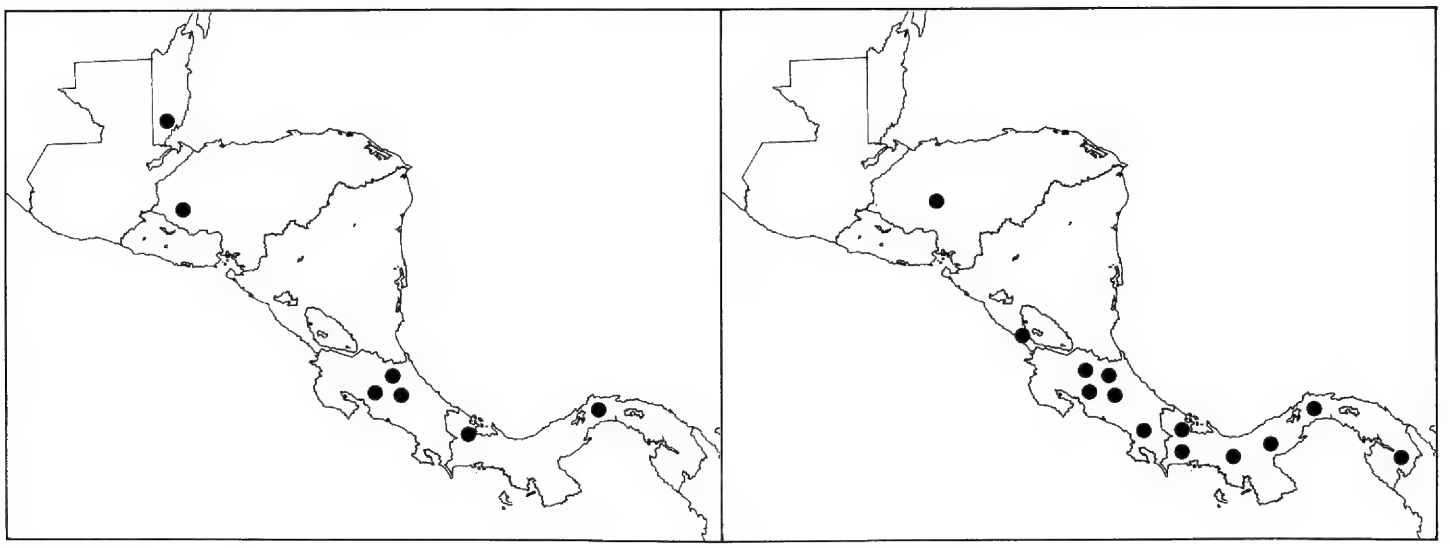


Figure 141. *Leskeodon auratus*. A. Habit. B. Seta, capsule, and operculum. C. Leaf apex. D. Exostome, dorsal (outer) surface. E. Calyptra. F & K. Leaves. G. Exothecial cells. H. Stem in cross section. I. Basal and alar cells. J. Rhizoidal propagulae. Scale in mm: bar = 0.06 (C, D, G–I); bar = 0.17 (J); bar = 0.28 (B); bar = 0.5 (E, F, K, L); bar = 1.3 (A). J from *Crosby 10044*; all other figure parts from *Allen 11532*.



Leskeodon auratus *Leskeodon cubensis*

In Central America *L. auratus* can be confused with *L. andicola* and *L. palmarum* since all three species have similar upper leaf cells. The typical form of *L. andicola* differs from *L. auratus* in having leaves that are crispate and wavy when dry. However, the *mexicanus*-form of *L. andicola* has leaves stiffly curled and contorted when dry and is similar to *L. auratus* in size, leaf shape, and leaf stance. All forms of *L. andicola* differ from *L. auratus* in having enlarged, thin-walled and bulging, oblong basal leaf cells with the basal juxtacostal cells especially enlarged. In contrast, the oblong basal leaf cells of *L. auratus* are enlarged but usually firm-walled, and the juxtacostal basal cells are not greatly enlarged and strongly differentiated from the outer basal cells. *Leskeodon palmarum* and *L. auratus* are identical in color, plant aspect, and leaf form. Both species also have densely branched rhizoids. *Leskeodon palmarum* differs from *L. auratus* in having fusiform-elongate, usually porose basal cells, consistently papillose rhizoids, longer setae, and longer capsules. Furthermore, the exothecial cells of *L. palmarum* are collenchymatous only in the upper one-third, the exostome teeth are more or less smooth, and the spores are larger (20–28 µm vs. 10–16 µm) than those of *L. auratus*. *Leskeodon cubensis* is not likely to be confused with *L. auratus*, because it has homogenous leaf cells, thin-walled but distinctly collenchymatous upper leaf cells, and often piliferous leaves.

3. *Leskeodon cubensis* (Mitt.) Thér., Mem. Soc. Cub. Hist. Nat. "Felipe Poey" 14: 364. 1940. *Distichophyllum cubense* Mitt., J. Linn. Soc., Bot. 12: 395. 1869. *Mniadelphus cubensis* (Mitt.) Müll. Hal. *ex* A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 318. 1877. Protologue. Ins. Cuba, ad arborum corticem, *Wright, n. 87.*

Distichophyllum elongatum Mitt., J. Linn. Soc., Bot. 12: 395. 1869. *Leskeodon elongatus* (Mitt.) S. P. Churchill & Linares, Bibliot. José Jerónimo Triana 12: 307. 1995. Protologue. [Colombia] Andes Bogotenses, Boquerón prope Bogotá (8600 ped.), ad rupes roridas, *Weir, n. 368.*

Distichophyllum longipilum Besch., J. Bot. (Morot) 16: 8. 1902. *Leskeodon longipilus* (Besch.) E. B. Bartram, Bull. Brit. Mus. (Nat. Hist.), Bot. 2(2): 45. 1955. Protologue. Guadeloupe, sur les arbres pourris, vallée de Saint-Louis (*P. Duss, n°1817*).

Plants small or medium-sized, 3–15(–25) mm tall, glossy, green to yellowish green, in tufts or thin to dense mats. Stems erect, sparsely and irregularly branched, somewhat complanate-foliate, dark red; stems in cross section with epidermis of 1–2 rows of small, thin-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs (3–)4–6 cells long, basal cell short-rectangular, reddish brown, upper 3–5 cells oblong-elongate, hyaline; rhizoids at base of stems, around branch primordia, and on stems abaxial to the leaf insertions, smooth, reddish brown, often pinnately branched. Leaves erect, curled-contorted to spirally twisted when dry, lateral leaves wide-spreading when wet, ventral and dorsal leaves smaller than the lateral leaves, erect to erect-spreading when wet, ovate, obovate, oblong, or spathulate, 1.0–2.5 mm long, acute to broadly rounded, apiculate, cuspidate, or piliferous, apices often twisted, decurrent;

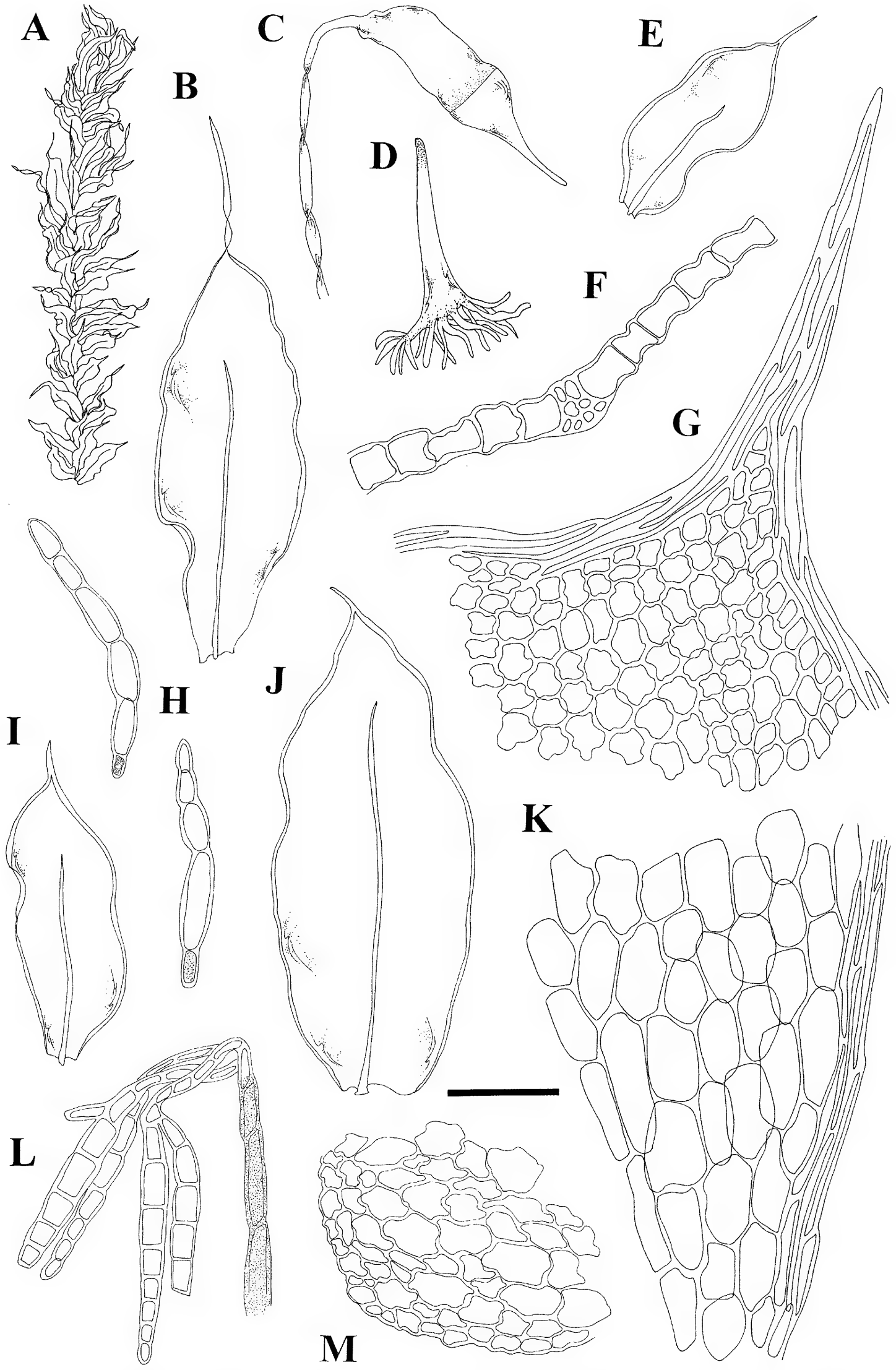


Figure 142. *Leskeodon cubensis*. A. Habit. B, E, I & J. Leaves. C. Seta, capsule, and operculum. D. Calyptra. F. Costa in cross section. G. Leaf apex. H. Axillary hairs. K. Basal and alar cells. L. Rhizoidal propagulae. M. Stem in cross section. Scale in mm: bar = 0.06 (F, G, K); bar = 0.08 (H, L); bar = 0.13 (M); bar = 0.5 (D); bar = 0.6 (B, C, E, I, J); bar = 1.56 (A). A, K from *Allen 13879*; B from *Cerda GC-1670*; I from *Lyon 248*; all other figure parts from *Crosby & Crosby 5976*.

margins entire, bordered completely by 2–3 rows of elongate cells, plane; costae single, slender, ending 1/2–3/4 the leaf length, in cross section cells homogeneously thick-walled; upper cells rounded or hexagonal, 16–30 µm long, smooth, thin-walled, usually collenchymatous, median cells similar but somewhat larger; basal cells enlarged, thin-walled, occasionally somewhat bulging, oblong, juxtacostal basal cells longer and broader, cells across the insertions enlarged, irregularly rectangular to subquadrate, reddish brown. Asexual reproduction occasionally by rhizoidal propagula. Autoicous or synoicous. Perichaetia and perigonia lateral on stems. Setae elongate, 3–6 mm long, red, smooth. Capsules erect, ovoid to short-cylindric, constricted at the neck, symmetric, 0.8–1.0 mm long; exothecial cells at the mouth red, short-rectangular, in 2–3 rows, lower cells subrectangular to rectangular, not or weakly collenchymatous; stomata on neck; opercula conic-rostrate, 0.6–1.0 mm long; annuli rudimentary, persistent; peristome diplolepideous; exostome teeth pale yellow to white, erect-recurved when wet, erect-incurved when dry, narrowly triangular, dorsal surface broader than ventral surface, papillose throughout, dorsal trabeculae and median line thin, ventral trabeculae strongly thickened and long-projecting; endostome as long or longer than the exostome teeth, yellowish to white, papillose, basal membranes low, segments broad, weakly keeled, not perforate, cilia rudimentary or absent. Spores rounded, 10–12 µm, lightly papillose. Calyptrae mitrate, smooth or roughened-papillose above, fimbriate at base, 1.0–1.3 mm long.

Illustrations. Thériot (1940, Pl. 55 1); Welch (1969, Figs. 214–221); Welch (1971b, Figs. 226–230); Sharp *et al.* (1994, Fig. 579 d–g, not Fig. 579 a–c); Churchill and Linares (1995, Fig. 57 e–g); Duarte Bello (1997, Pl. 235); Buck (1998, Pl. 4). Figure 142.

Habitat. On roots, fern trunks, small bushes, tree trunks, branches, and twigs, epiphytic on dicot leaves, palm fronds, and fern fronds, on rotting wood, stumps, humus along stream banks, and on rocks along streams; 350–2100 m.

Distribution in Central America. HONDURAS. Comayagua: *Allen 13879* (MO). NICARAGUA. Rivas: *Granzow de la Cerda GC-1670* (DUKE, MO). COSTA RICA. Alajuela: *Crosby 9971* (MO); Cartago: *Crosby & Crosby 5812* (MO); Heredia: *Crosby & Crosby 6585* (CR, F, FH, MO, NY, US); Puntarenas: *Lyon 338* (MO); San José: *Crosby 9726* (MO). PANAMA. Bocas del Toro: *Allen 5627* (MO); Chiriquí: *Allen 5485* (MO); Coclé: *Lewis et al. 1717* (MO); Darién: *Folsom 4282A* (MO); Panamá: *Crosby 10084* (MO, NY, PMA, US); Veraguas: *Crosby 10277a* (MO).

World range: Mexico; Central America; Caribbean; Western and Northern South America.

Leskeodon cubensis is often epiphyllous or grows on twigs, and in this habitat it is usually a small, loosely tufted species with spirally twisted, ovate to spathulate leaves. It also grows on stream banks or rocks along streams, where the plants are considerably larger, occur in dense mats, and have contorted, oblong leaves with undulate margins. The epiphyllous form of *L. cubensis* typically has piliferous leaves and is sometimes recognized at the species level as *L. longipilus*. The larger, mat-forming collections are often apiculate to cuspidate. Although the two forms are often quite distinct, the presence of many morphologically intermediate collections makes the recognition of two species unwarranted.

All forms of *L. cubensis* have leaves with plane, entire margins and weak costae that end 1/2–3/4 the leaf length. *Leskeodon cubensis* has exceptionally large upper leaf cells that are rounded to hexagonal, thin-walled, and usually collenchymatous. The degree of collenchymatous leaf cell thickening varies from one collection to another and even from leaf to leaf on single collections. The basal leaf cells are oblong and considerably larger than the upper leaf cells, but, because there is a gradual transition between them, the areolation is homogeneous in appearance. Sporophytically, *L. cubensis* has short, smooth setae and ovoid to short-cylindric capsules with weakly collenchymatous exothecial cells.

Leskeodon paisa and *L. andicola* are the only Central American species of *Leskeodon* likely to be confused with *L. cubensis*, because all three species have enlarged, thin-walled basal leaf cells. *Leskeodon paisa* and *L. cubensis* also have large, thin-walled upper leaf cells and "net-like" areolation similar to that of *Cyclodictyon*. *Leskeodon paisa* differs from *L. cubensis* in having orbicular, apiculate leaves and non-collenchymatous leaf cells. *Leskeodon andicola* differs most clearly from *L. cubensis* in having small (10–14 µm long), firm-walled upper leaf cells. In addition, the basal leaf cells in *L. andicola* are abruptly differentiated from the upper/median cells; the juxtacostal basal cells are abruptly enlarged, strongly differentiated from the outer basal leaf cells; and its leaves are mucronate to cuspidate, but never piliferous.

4. *Leskeodon paisa* S. P. Churchill *in* I. Sastre, S. P. Churchill & M. Escobar, Actual. Biol. 15: 88. 1986. Protologue. Colombia, departmento de Antioquia, municipio de Sonsón: 9.5 km E de Sonsón hacia Nariño y Argelia, ca. 2660 m, ca. 05°40′N, 75°15–20′W, bosque pluvial montano, laderas del bosque y a orillas de quebrada con piedras grandes, *Churchill y Sastre-D. J. 12945*. Type. Colombia. Antioquia, Municipio Sonsón. 9.5 km E de Sonsón hacia Nariño y Argelia. 2660 m. Bosque Pluvial Montano, laderas del bosque y a orillas de quebrada con piedras grandes, Junio 22 1985, *Steven Churchill e Inés Sastre-De Jesús 12945* (MO, isotype).

Plants small, 2–6 mm tall, glossy, yellowish green, in dense mats. Stems erect, sparsely and irregularly branched, somewhat complanate-foliate, dark red; stems in cross section with thin-walled cells throughout, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 3 cells long, basal cell short-rectangular, reddish brown, upper cells oblong-elongate, hyaline; rhizoids at base of stems, around branch primordia, and on stems abaxial to the leaf insertions, smooth to lightly roughened, reddish brown, often pinnately branched. Leaves erect, curled-contorted when dry, lateral leaves wide-spreading when wet, ventral and dorsal leaves smaller than the lateral leaves, erect to erect-spreading when wet, orbicular, 0.7–1.0 mm long, broadly rounded, apiculate, apices at times twisted when dry, decurrent; margins entire, bordered completely by 2–3 rows of elongate cells, plane; costae single, slender, ending 1/2–3/4 the leaf length, in cross section cells homogeneously thick-walled; upper cells rounded to rhombic or hexagonal, 16–20 µm, smooth, thin-walled, not collenchymatous, median cells similar but somewhat larger; basal cells enlarged, thin-walled, occasionally somewhat bulging, hexagonal to oblong, 30–50 µm, juxtacostal basal cells larger, bulging, cells across the insertions enlarged, irregularly rectangular to subquadrate, reddish brown. Asexual reproduction not seen. Sporophytes unknown.

Illustrations. Sastre-De Jesús *et al.* (1986, Fig. 11); Churchill and Linares (1995, Fig. 57 h–i). Figure 143.

Habitat. On small twigs; 3130 m.

Distribution in Central America. COSTA RICA. San José: *Crosby & Crosby 5831* (MO).

World range: Central America; Western South America.

Leskeodon paisa is a small species that grows in dense mats. The plants are glossy, yellowish green to green, and have orbicular leaves that are stiffly erect-curled when dry. The species has broadly rounded, apiculate leaf apices and margins that are plane and hyaline-bordered throughout. The upper leaf cells of *L. paisa* are rounded to hexagonal, with thin, non-bulging walls, while the basal cells are enlarged, sometimes bulging. The basal juxtacostal cells are even more enlarged and usually bulging.

Leskeodon paisa is more likely to be confused with *L. cubensis* than with any other Central American species of *Leskeodon*. This is because their leaf cells are similar in form and in having thin walls. Indeed, the leaf areolation in these two species is "net-like," a form often associated with *Cyclodictyon*. *Leskeodon cubensis* differs from *L. paisa* in having ovate to obovate leaves and leaf cells that are often collenchymatous. Furthermore, the most common Central American form of *L. cubensis* has piliferous leaves. *Leskeodon andicola* is somewhat similar to *L. paisa* in having thin-walled, bulging, oblong basal leaf cells with even more enlarged basal juxtacostal cells. It differs from *L. paisa* in having ovate to oblong-ovate leaves, with undulate margins and firm-walled upper leaf cells.

5. *Leskeodon palmarum* (Mitt.) Broth., Nat. Pflanzenfam. I(3): 926. 1907. *Distichophyllum palmarum* Mitt., J. Linn. Soc., Bot. 12: 394. 1869. *Mniadelphus palmarum* (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 318. 1877. Protologue. [Ecuador] Andes Quitenses, in sylva Canelos ad palmarum truncos (4000 ped.), *Spruce, n. 570.*

Distichophyllum mariei Besch., Rev. Bryol. 18: 77. 1891. *Dissodon mariei* (Besch.) Besch. *ex* Paris, Index Bryol. Suppl. 129. 1900. *Leskeodon mariei* (Besch.) Broth., Nat. Pflanzenfam. I(3): 926. 1907. Protologue. Guadeloupe, à la Soufrière, *Ed. Marie*, mars-mai 1877, *n° 48.*

Leskeodon caducifolius W. R. Buck, A. J. Shaw & C. Cox, Brittonia 54: 178. 2002. Protologue. Ecuador. Prov. Loja: Parque Nacional Podocarpus, 9 km SE of park entrance along Hwy 39, S of city of Loja, Sendero

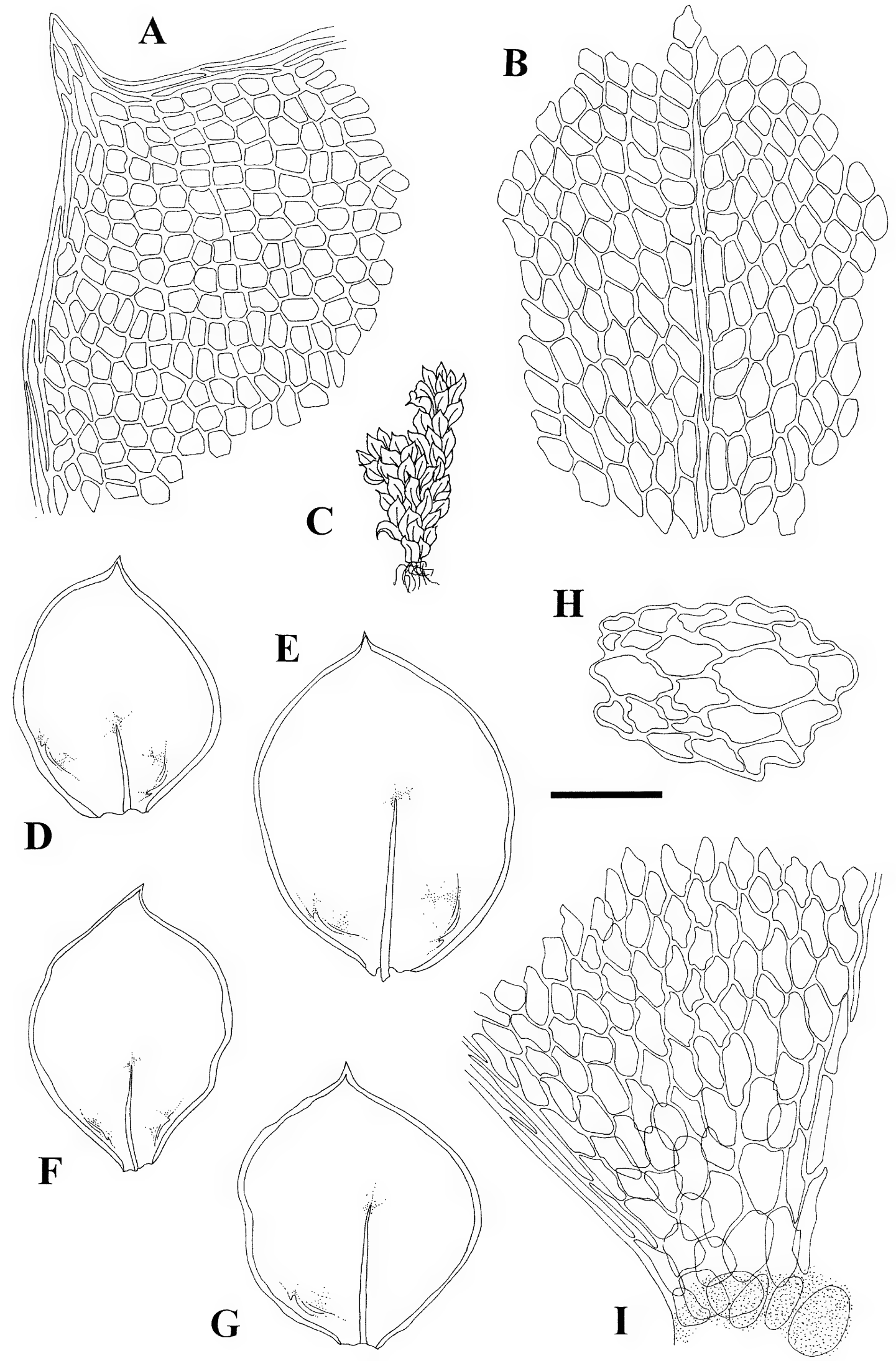
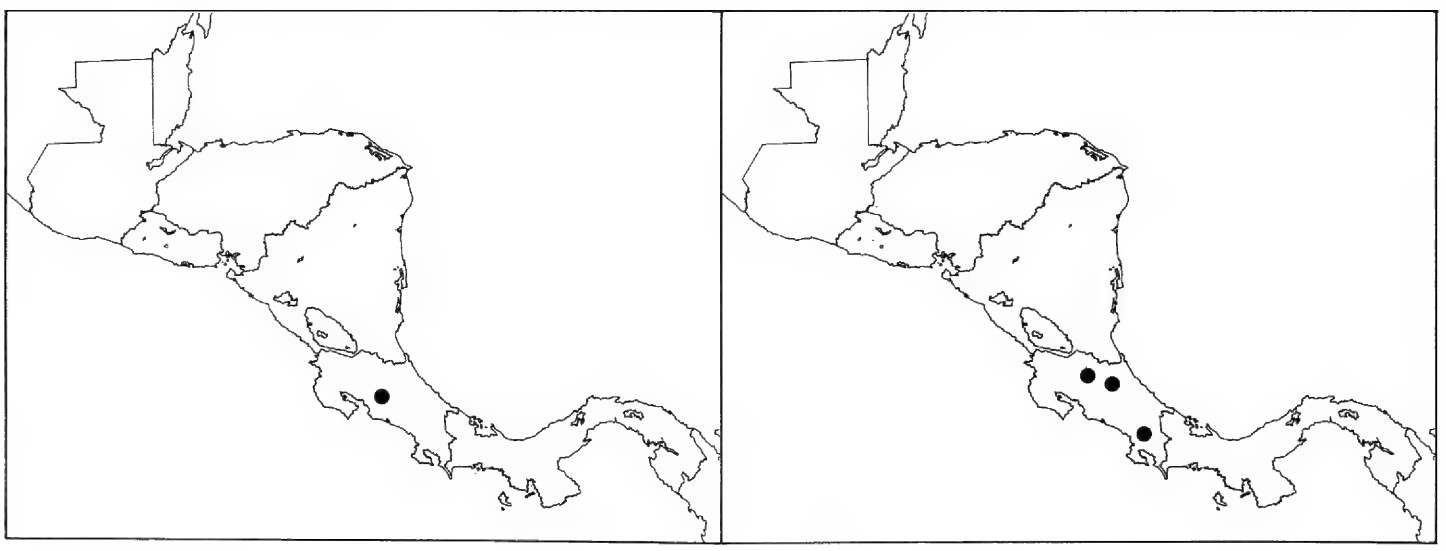


Figure 143. *Leskeodon paisa*. A. Leaf apex. B. Upper cells and upper part of costa. C. Habit. D, E, F & G. Leaves. H. Stem in cross section. I. Basal and alar cells. Scale in mm: bar = 0.06 (A, B, H, I); bar = 0.28 (D–G); bar = 1.3 (C). All figure parts from *Crosby & Crosby 5831*.



Leskeodon paisa *Leskeodon palmarum*

Autoguiado Bosque Nublado, from Cajanuma, ca. 4°04′S, 79°09′W, ca. 2750–2800 m; montane cloud-forest, on underside of slanting tree; 28 May 2001, *W. R. Buck 39582*. Type. Ecuador. Prov. Loja: Parque Nacional Podocarpus, 9 km SE of park entrance along Hwy 39, S of city of Loja, Sendero Autoguiado Bosque Nublado, from Cajanuma, ca. 4°04′S, 79°09′W, ca. 2750–2800 m; montane cloud forest. On underside of slanting tree trunk, 28 May 2001, *William R. Buck 39582* (MO, isotype), *syn. nov.*

Plants small to medium-sized, 3–15 mm long, glossy, yellowish green to reddish yellow, in dense mats. Stems erect, sparsely and irregularly branched, somewhat complanate-foliate, dark red; stems in cross section with epidermis of 1–2 rows of small, thick-walled, red cells, cortical cells enlarged, thick-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2–3 cells long, basal cell short-rectangular, reddish brown, upper 1–2 cells oblong-elongate, hyaline; rhizoids at base of stems, around branch primordia, and on stems abaxial to the leaf insertions, roughened-papillose, reddish brown, densely pinnately branched. Leaves erect, curled-contorted when dry, fragile and often caducous; lateral leaves wide-spreading when wet, ventral and dorsal leaves smaller than the lateral leaves, erect to erect-spreading when wet, ovate, obovate, oblong-ovate, or spathulate, 1–1.5 mm long, acute to broadly rounded, apiculate, apices at times twisted, decurrent; margins entire, bordered completely by 2–4 rows of elongate cells, plane; costae single, slender, ending at or little above midleaf, in cross section at base with enlarged ventral surface, other cells homogeneously thick-walled; upper cells rhomboidal, rhombic, hexagonal, or rounded, 12–24 × 8–10 µm, smooth, thick-walled, usually porose, median cells similar but somewhat larger; basal cells fusiform-elongate, thick-walled, not bulging, porose, cells across the insertions enlarged, irregularly rectangular to subquadrate, reddish brown. Asexual reproduction by caducous leaves and occasionally by rhizoidal propagula. Autoicous. Perichaetia and perigonia lateral on stems. Setae elongate, 6–12 mm long, flexuose, red, roughened above, smooth below. Capsules erect, cylindric, constricted at the neck, symmetric, 0.5–1.0 mm long; exothecial cells at the mouth short-rectangular, in 2–3 rows, lower cells in upper 1/3 of the capsule larger, rounded-quadrate, collenchymatous, cells in lower 2/3 short-rectangular, not collenchymatous; stomata on neck; opercula conic-rostrate, 0.8 mm long; annuli rudimentary, persistent; peristome diplolepideous; exostome teeth pale yellow to white, erect-recurved when wet, erect-incurved when dry, narrowly triangular, dorsal surface smooth or obscurely papillose, dorsal trabeculae and median line thick, ventral trabeculae faint; endostome yellowish white, papillose, basal membranes low, segments broad, faintly keeled, not perforate, cilia absent. Spores rounded, 22–28 µm, lightly papillose. Calyptrae mitrate, roughened-papillose above, often with a few thick, ascending hairs, fimbriate at base, 1.0–1.4 mm long.

Illustrations. Brotherus (1907a, Fig. 677); Brotherus (1925, Fig. 595); Welch (1972a, Figs. 229–238); Buck (1998, Pl. 2 1–4); Buck *et al.* (2002, Figs. 1–8). Figure 144.

Habitat. On tree trunks and rotting logs; 1500–2100 m.

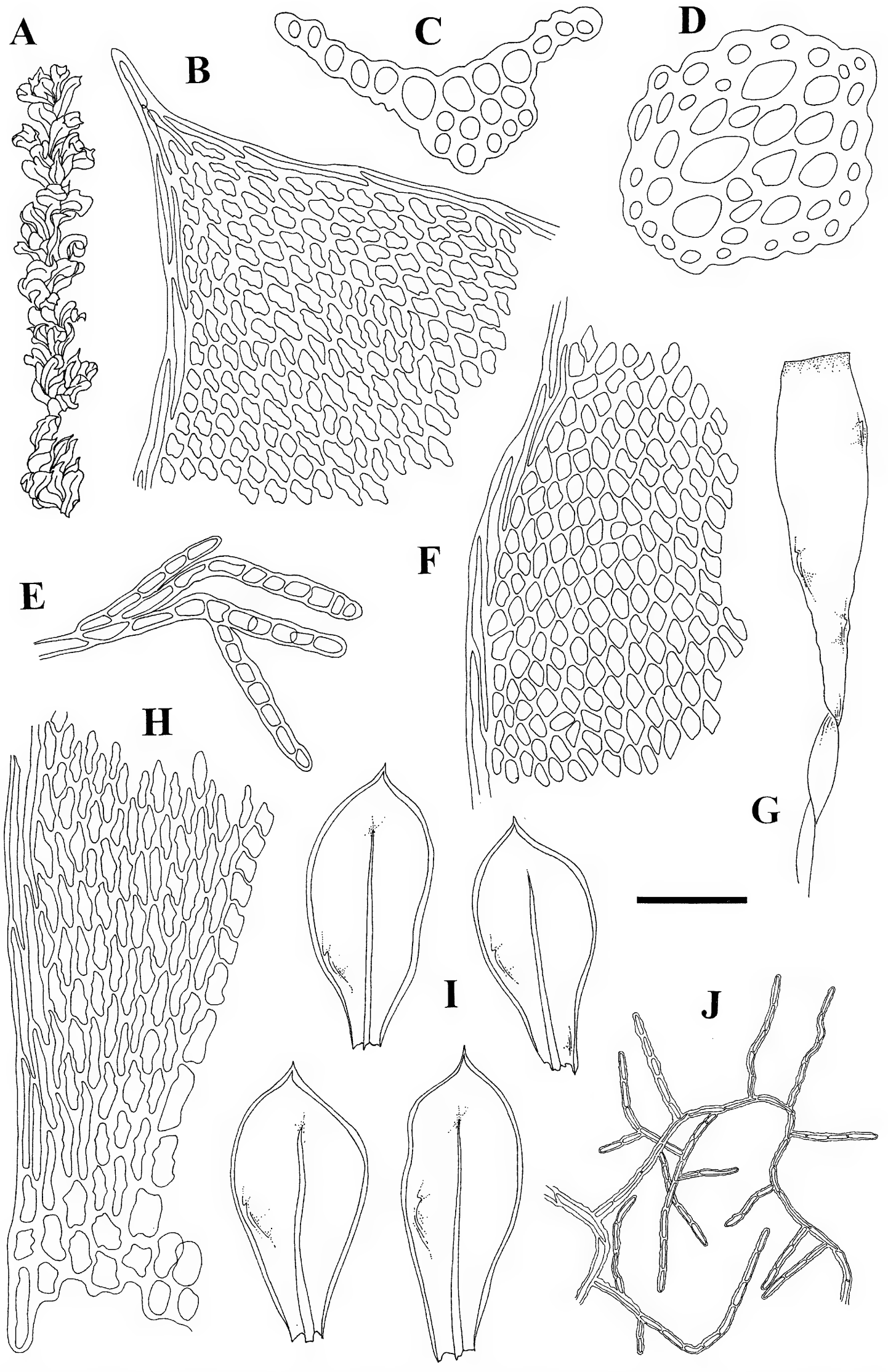


Figure 144. *Leskeodon palmarum*. A. Habit. B. Leaf apex. C. Costa in cross section. D. Stem in cross section. E. Rhizoidal propagulae. F. Median leaf cells and margin. G. Seta and capsule. H. Basal and alar cells. I. Leaves. J. Rhizoids. Scale in mm: bar = 0.05 (C); bar = 0.06 (B, D, F, H); bar = 0.09 (E); bar = 0.17 (J); bar = 0.5 (G, I); bar = 1.56 (A). All figure parts from *Lyon 462*.

Distribution in Central America. COSTA RICA. Alajuela: *Crosby 9990* (CR, MO); Heredia: *Crosby & Crosby 5982* (MO); Puntarenas: *Lyon 462* (CR, F, FH, MO, NY).

World range: Central America; Caribbean; Western South America.

Leskeodon palmarum is often a medium-sized species that grows in dense mats. The plants are glossy and usually yellowish red, with dense, papillose, pinnately branched rhizoids, and dark red leaf borders and costae. The leaves are stiffly erect-curled when dry, often fragile and caducous. They have rounded-apiculate apices with plane, strongly bordered margins. The upper leaf cells of *L. palmarum* are thick-walled, often porose, and characteristically long-rhomboidal, but sometimes (especially those of the dorsal and ventral leaves) they can be rounded to hexagonal or rhombic. The basal cells are elongate-fusiform, thick-walled, and nearly always porose. Sporophytically, *L. palmarum* has longer setae than any other Central American species of *Leskeodon*, and cylindric capsules that have collenchymatous exothecial cells restricted to the upper one-third of the capsule. The exostome teeth of *L. palmarum* are broader than those of other regional *Leskeodon* species, and they are more or less smooth on the dorsal surface. The spores of *L. palmarum* are the largest of any *Leskeodon* species in Central America. Indeed, *L. palmarum* is distinctly different from the other members of *Leskeodon*, and this is reflected by its placement in its own section: *Leskeodon* sect. *Longiseti* Broth. In plant color and aspect, as well as its densely branched rhizoids and porose leaf cells, *L. palmarum* is remarkably similar to *Adelothecium bogotense*, but that species is considerably larger than *L. palmarum*.

In Central America *L. palmarum* is likely to be confused only with *L. auratus*: both occur in dense mats; both have pinnately branched rhizoids; and both are yellowish red plants with leaves that are stiffly curled and contorted when dry. The long rhomboidal leaf cells of *L. palmarum* will often distinguish it from *L. auratus*, which has short, rounded upper leaf cells. However, the upper leaf cells of *L. palmarum* are variable in size and shape; at times they are identical to those of *L. auratus*. The best gametophytic difference between these species is found in their basal leaf cells. *Leskeodon auratus* has enlarged, oblong basal leaf cells that are distinctly different from the fusiform-elongate, thick-walled, nearly always porose basal leaf cells of *L. palmarum*. Sporophytically, *Leskeodon auratus* differs from *L. palmarum* in having shorter setae and subcylindric capsules that in the upper two-thirds are collenchymatous. Furthermore, the exostome teeth of *L. auratus* are thinner than those of *L. palmarum* and densely papillose throughout, while the spores are considerably smaller (12–16 µm vs. 22–28 µm). *Leskeodon cubensis* is not likely to be confused with *L. palmarum*. It differs in having homogenous leaf cells and upper leaf cells that are thin-walled, but distinctly collenchymatous. In addition, the most common form of *L. cubensis* has piliferous leaves. *Leskeodon andicola* differs from *L. palmarum* in having enlarged, thin-walled and bulging, oblong basal leaf cells, with the basal juxtacostal cells especially enlarged.

HOOKERIACEAE

Hookeriaceae Schimp., Coroll. Bryol. Eur. 101. 1856.

Hookeriaceae subfam. Hookeriopsidoideae H. A. Mill., Phytologia 21: 248. 1971.

Plants small, medium-sized, or robust in pale green, green, golden, or reddish mats or tufts. Stems prostrate, ascending, or pendent, often complanate-foliate, sparsely or 1–2-pinnately branched, lightly pigmented when young, becoming reddish with age; stems in cross section with hyalodermis or sclerodermis, firm-walled cortical cells, central strand typically absent, occasionally rudimentary to weakly developed; branch primordia scattered over the stems or in leaf axils, typically with scale leaves, occasionally with foliose or subfoliose pseudoparaphyllia; axillary hairs 2(–3) cells long, hyaline or with the basal cell pigmented; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves monomorphic or dimorphic, with often asymmetric lateral leaves larger than the symmetric dorsal and ventral leaves, lanceolate to broadly ovate or obovate; costae double, variable in length but usually long and ending above mid-leaf, occasionally absent; margins usually serrulate or serrate, occasionally dentate or entire, often with a border of elongate cells; cells isodiametric, hexagonal, elongate-rhomboidal, rectangular, or linear, smooth, papillose, or prorate; alar cells not differentiated. Gemmae often produced on stems, typically from clusters of initials abaxial to the leaf insertions. Autoicous, synoicous, or dioicous. Gametangia on short lateral branches on stems or branches. Setae long or short, smooth, papillose, or spinose. Capsules erect or inclined; exothecial cells often collenchymatous; stomata rudimentary, 2–6-celled, on neck; opercula conic-rostrate; annuli often massive, of 5–20 rows of yellowish, quadrate to hexagonal cells separating from capsule along dehiscent zone at base, persistent on the operculum; peristome diplolepideous: hookeriaceous (exostome teeth narrowly triangular with broad median furrow, densely and closely striate below, coarsely papillose above, dorsal surface dark red, ventral surface hyaline to yellowish, lightly papillose; endostome as high as the exostome, yellowish, lightly papillose, basal membranes high, segments broad, strongly keeled, not or weakly perforate, cilia absent or rudimentary) or daltoniaceous (exostome teeth very narrowly triangular, median furrow absent, dorsal surface broad, whitish yellow, lightly papillose throughout, trabeculae thin, median line faint, ventral surface narrow, 1/3 or less the width of the dorsal surface, red or yellow, lightly papillose, deposition thick; endostome as high as the exostome, pale yellowish, papillose throughout, basal membranes high, segments broad, concave-keeled, not perforate, cilia absent or rudimentary). Calyptrae mitrate or campanulate-mitrate, often lobed or laciniate-fringed at base, often variously hairy, often papillose-roughened.

The Hookeriaceae are a large and diverse, primarily tropical or subtropical, family. There has been considerable controversy over the makeup of the Hookeriaceae, primarily due to the presence of a large number of generic pairs that have very similar gametophytes but radically different sporophytes. Crosby (1974b), emphasizing sporophytic similarity, restricted the family to those genera having a hookeriaceous peristome: exostome teeth with broad median furrow, densely and closely striate on lower dorsal surface; endostome basal membranes high, segments broad, strongly keeled, not or weakly perforate, cilia absent. Buck (1987, 1988, 1998) narrowly restricted the Hookeriaceae to include only members of the Hookeriales with a weak stem central strand, elimbate leaves with large, lax cells, and weak or absent costae, smooth setae, and cross-striate exostome teeth. Most genera treated here in the Hookeriaceae were positioned by Buck (1987, 1988, 1998) in the Pilotrichaceae. His treatment of that family emphasized gametophytic similarities and included genera with either a daltoniaceous or hookeriaceous peristome. Buck placed genera in the Pilotrichaceae that usually had a stem sclerodermis, lacked a stem central strand, and had leaves with strong, double costae. Buck *et al.* (2003) evaluated the Hookeriales using a combination of molecular and morphological techniques. This study restricted the Hookeriaceae to the ecostate genera *Crossomitrum* and *Hookeria*, and a large Pilotrichaceae again consisting of most of the genera here placed in the Hookeriaceae.

Whittemore and Allen (1989) also examined the Hookeriaceae problem from a gametophytic perspective. They noted that the different peristome morphologies within the Hookeriales were cor-

related with important functional differences: hookeriaceous peristome xerocastique, *i.e.*, reflexed when dry and incurved when wet; daltoniaceous peristome hygrocastique, *i.e.*, incurved when dry and outcurved when wet. They concluded, on the basis of their observations, that the daltoniaceous peristome did not exhibit uniform morphology. In addition, because of the lack of correlation within the Hookeriales between characters of the peristome and gametophytic features, they considered the daltoniaceous peristome to have arisen more than once in the order. In their view the Hookeriaceae represented a group of mosses with usually bicostate leaves (rarely ecostate); rhizoids unbranched (occasionally sparsely and irregularly branched) and densely clustered abaxial to the leaf insertions; axillary hairs 2(–3) cells long; plants always branched; stem cortex weakly pigmented; and mitrate, usually lobed, calyptrae. The circumscription of the Hookeriaceae and disposition of genera proposed by Whittemore and Allen (1989) is followed here.

An outstanding feature of many genera in the Hookeriaceae is the presence of a massive annulus that consists of 5–20 rows of yellowish, quadrate to hexagonal cells separating from the capsule along a basal dehiscent zone and persistent on the operculum. This feature was first noted and described by Buck (1992) for *Philophyllum tenuifolium* and *Leucomium strumosum*. Buck was unsure whether the feature had an annular or opercular origin, and he found these cells were thin-walled on the outer surface, thick-walled on the inner surface, and had 1–3 elongate, rib-like thickenings on the inner anticlinal and periclinal walls. This distinctive annulus occurs in *Brymela*, *Callicostella*, *Crossomitrium*, *Lepidopilidium*, *Lepidopilum*, *Philophyllum*, *Stenodictyon*, *Thamniopsis*, and *Trachyxiphium*. As noted by Buck (1992), it is also found in the Leucomiacae. The gametophytes of most species of the Hookeriaceae often display a remarkable degree of variation. At times this variation is associated with leaf dimorphism, but at other times it appears to be environmentally induced, due to growth in very wet, low light intensity places. When plants that normally have dimorphic leaves are also affected by environmental conditions, the resulting morphological variations can be astounding. As a result of this incredible variability, keys to genera as well as keys to species often fail to adequately separate the taxa. The following key is primarily based on the key to the genera of Pilotrichaceae in Buck (1998).

1. Leaf costa absent or short and double, less than 1/4 the leaf length 2
1. Leaf costa present, reaching to or above midleaf 4

2. Leaves uni- or biserrate to bidentate; asexual brood bodies on stem and leaf bases or on specialized brood branches; calyptrae fimbriate at base by uniseriate, multicellular hairs . . . . . 5. *Crossomitrium*
2. Leaves entire or obscurely serrulate; asexual brood bodies on leaf apices and marginal cells or absent; calyptrae entire at base 3

3. Leaves slenderly long-acuminate; median leaf cells linear-flexuose, 10–14 µm wide; costae often short and double . . . . . 12. *Philophyllum*
3. Leaves acute to broadly acute; median cells elongate-hexagonal to rhomboidal, 41–62 µm wide; costae absent or present only as a basal bistratose region . . . . . 8. *Hookeria*

4. Leaves strongly bordered 5
4. Leaves not or obscurely bordered 7

5. Upper leaf cells firm-walled (but see *L. diaphanum*), hexagonal to elongate-fusiform; costae usually ending near or below midleaf . . . . . 11. *Lepidopilum p.p.*
5. Upper leaf cells lax, broadly hexagonal; costae 2/3–3/4 the leaf length 6

6. Dorsal surface of exostome teeth lacking median furrow, papillose throughout . . . . . 2. *Amblytropis*
6. Dorsal surface of exostome teeth with broad median furrow, densely cross-striate at base . . . . . 6. *Cyclodictyon*

7. Leaf cells papillose or prorate 8
7. Leaf cells smooth 13

8. Leaf cells pluripapillose 9
8. Leaf cells prorate or unipapillose 10

9. Leaf cells isodiametric, costae thick and very strong, often converging at the tips; leaf margins entire . . . . . 13. *Pilotrichidium p.p.*
9. Leaf cells elongate, costae well developed, but not exceptionally thick, divergent or parallel throughout; leaf margins typically serrulate to serrate . . . . . 9. *Hypnella*

10. Leaf cells papillose . . . . . 4. *Callicostella p.p.*
10. Leaf cells prorate 11

11. Leaf margins with swollen, bifid teeth . . . . . 17. *Trachyxiphium p.p.*
11. Leaf margins entire to serrate, teeth unswollen 12

12. Leaf cells elongate, often porose; costae relatively weak, 2/3–3/4 the leaf length . . . . . 3. *Brymela p.p.*
12. Leaf cells isodiametric to oblong; rarely porose; costae strong, ending near the apex . . . . . 4. *Callicostella p.p.*

13. Leaves strongly plicate . . . . . 7. *Hemiragis*
13. Leaves not or weakly plicate 14

14. Primary stems erect 15
14. Primary stems prostrate 16

15. Leaf margins tightly recurved; exothecial cells evenly thickened; setae smooth; calyptrae naked . . . . . 1. *Actinodontium*
15. Leaf margins plane or weakly recurved; exothecial cells often collenchymatous; setae spinose; calyptrae with multiseriate hairs . . . . . 11. *Lepidopilum p.p.*

16. Leaf cells isodiametric; costae thick and very strong, often converging at the tips; leaf margins entire . . . . . 13. *Pilotrichidium p.p.*
16. Leaf cells elongate; costae well developed, but not exceptionally thick, divergent or parallel throughout; leaf margins serrulate, serrate OR entire 17

17. Leaves abruptly constricted at base of acumina or subulate 18
17. Leaves rounded, acute, or gradually acuminate 20

18. Leaf margins sharply serrate or with large, swollen teeth . . . . . 16. *Thamniopsis p.p.*
18. Leaf margins entire, subentire, or obscurely sinuate above 19

19. Dorsal surface of exostome teeth lacking median furrow, papillose throughout . . . . . 14. *Stenodesmus*
19. Dorsal surface of exostome teeth with broad median furrow, densely cross-striate at base . . . . . 15. *Stenodictyon*

20. Stems with a sclerodermis 21
20. Stems with a hyalodermis 22

21. Leaf margins often with paired, bifid teeth; cells thin-walled; costae spined, often crested with paired, bifid teeth at back . . . . . 17. *Trachyxiphium p.p.*
21. Leaf margins with single teeth; cells firm-walled; costae not or weakly spined, smooth at back . . . . . 3. *Brymela p.p.*

22. Costae strong, ending above midleaf, often projecting, crested or toothed . . . . . 16. *Thamniopsis p.p.*
22. Costae weak, ending at or below midleaf, not or rarely projecting 23

23. Dorsal surface of exostome teeth lacking median furrow, papillose throughout . . . . . 11. *Lepidopilum p.p.*
23. Dorsal surface of exostome teeth with broad median furrow, densely cross-striate at base . . . . . 10. *Lepidopilidium*

1. *Actinodontium* Schwägr., Sp. Musc. Frond. Suppl. 2(2)1: 75. 1826. *Lepidopilum* sect. *Actinodontium* (Schwägr.) Mitt., J. Linn. Soc., Bot. 12: 366. 1869.

Plants small to medium-sized, yellowish green to golden reddish, tufted. Stems erect or ascending, not or sparsely branched, evenly foliate or weakly complanate-foliate; stems in cross section with

incomplete hyalodermis, epidermis of smaller, thick-walled cells, enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2–3 cells long; rhizoids from scattered initials abaxial to the leaf insertions, not or sparsely and irregularly branched. Leaves erect to erect-spreading whether wet or dry, more or less symmetric, concave, oblong-lanceolate, gradually acute to short-acuminate, decurrent; margins entire throughout or serrulate at the apex, narrowly recurved throughout or in the lower 3/4, indistinctly bordered by 1–2 rows of narrow, elongate cells; costae double, 1/2–2/3 the leaf length; cells smooth, upper cells long-rhomboidal to long-hexagonal, firm-walled; basal cells near insertions rectangular, reddish across the insertions; alar cells undifferentiated, decurrency cells enlarged, oblong, thin-walled. Asexual reproduction by dense clusters of brood bodies borne in leaf axils. Heteroicous or dioicous. Setae elongate, smooth or somewhat roughened below the capsule. Capsules erect, cylindric, neck moderately developed; exothecial cells long-rectangular below, thick-walled, not collenchymatous; stomata rudimentary; opercula conic-rostrate; annuli rudimentary, deciduous; peristome diplolepideous; exostome teeth white, erect to recurved when wet, incurved when dry (hydrocastique), narrowly triangular, both surfaces papillose throughout, dorsal trabeculae and median lines weak, ventral trabeculae moderately developed; endostome white, spiculose-papillose above, basal membranes low, segments linear, keeled, not or faintly perforate, cilia absent. Calyptrae mitrate, irregularly lobed at base, naked, smooth.

Actinodontium is a genus of five species found in the Neotropics (2 species), Africa (1 species), and Southeast Asia (2 species). Tan and Robinson (1990) thought the Asian species may be synonymous, and in fact they also appear identical to *Actinodontium sprucei*, the most common Neotropical species. Plants of *Actinodontium* usually occur as scattered plants or sparse tufts on rotting logs or as epiphytes. They have a golden green color and are often bronze or reddish tinged. The genus is different from most other members of the Hookeriaceae in having erect or ascending primary stems and more or less evenly foliate leaves. The leaves are variably ovate-lanceolate, with long double costae, distinct decurrencies, and tightly recurved margins. A curious feature of the *Actinodontium* leaf is the presence of enlarged, bulging cells below the leaf insertions at the alar angles. Tan and Robinson (1990) interpreted these cells as stem epidermal cells that grow outward from the insertions, but they may actually be leaf decurrencies. Although the stems in cross section seem to have an incomplete hyalodermis, this too may be an artifact of the bulging decurrency cells. Additional unusual features of *Actinodontium* include the relatively sparse occurrence of rhizoids from scattered rhizoidal initials abaxial to the leaf insertions and the presence of brood bodies in the leaf axils. Sporophytically, *Actinodontium* is characterized by its elongate, mostly smooth setae, erect, cylindric capsules, and strongly hygrocastique peristome with completely papillose exostome teeth. The rudimentary stomata of *Actinodontium* are a distinctive feature of the capsule.

In Central America *Actinodontium* is distinguished from nearly all members of the Hookeriaceae by its erect, nearly unbranched primary stems. Most *Lepidopilum* species can be separated from *Actinodontium* by their creeping primary stems and distinctly complanate leaves that are strongly bordered. There is, however, a troublesome group of species (centered on *L. longifolium*) with a similar color, erect stems, and weakly to not complanate leaves. Furthermore, the group has leaves that are similar to those of *Actinodontium* in overall form as well as apex form and in having tightly recurved margins. Sporophytically, this group of *Lepidopilum* differs from *Actinodontium* in having densely papillose to hispid setae. It also has calyptrae with multiseriate hairs. Gametophytically, it can be distinguished from *Actinodontium* only in having leaves with longer, more narrowly acuminate apices, more weakly recurved leaf margins, and somewhat shorter costae. *Stenodictyon* also has non-complanate leaves, which gives it an aspect similar to *Actinodontium.* It differs, however, in having hair-pointed leaves with plane margins and exostome teeth that are densely cross-striate on the dorsal surface.

The name *Actinodontium* combines the Greek *actino* (star-like or radiating from a center) and *odontos* (tooth); it refers to the peristome teeth, which radiate outward when wet.

1. Plants to 7 mm high; leaves linear-lanceolate, narrowly acuminate to subulate, plane and serrulate above; rhizoids smooth . . . . . 1. *A. pygmaeum*
1. Plants 10–20 mm high; leaves oblong-lanceolate, gradually acute to short-acuminate, often narrowly revolute and entire to serrulate above; rhizoids roughened . . . . . 2. *A. sprucei*

1. ***Actinodontium pygmaeum*** W. R. Buck, Mem. New York Bot. Gard. 82: 48. 1998. Protologue. [Dominican Republic] Prov. La Vega: "La Laguna," along trail up Pico Duarte, 6370 feet, humid hardwood forest, ca. 19°02′N, 70°55′W, 13 Jan. 1987, *W. R. Buck 14131.* Type. Prov. La Vega: "La Laguna," along trail up Pico Duarte, 6370 feet, humid hardwood forest, ca. 19°02′N, 70°55′W, 13 January 1987, *William R. Buck 14131* (NY, holotype).

Plants small, 5–7 mm tall, yellowish green to golden reddish, in sparse tufts. Stems erect or ascending, not or sparsely branched, reddish, evenly foliate; stems in cross section with incomplete hyalodermis, subepidermis of 0–1(–2) rows of smaller, thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2–3 cells long, basal 1–2 cells short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from scattered initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect to erect-spreading whether wet or dry, more or less symmetric, somewhat concave, linear-lanceolate, 1.4–2.1 mm long, narrowly acuminate to subulate, decurrent; margins plane and serrulate at apex, entire to serrulate and weakly narrowly recurved below, not bordered; costae double, gradually divergent, 1/2 the leaf length; cells smooth, upper cells long-rhomboidal, 60–120 × 4–12 µm, firm-walled, more or less porose, lower cells longer and narrower, to 160 µm long; basal cells near insertions rectangular, reddish across the insertions; alar cells undifferentiated, 1–3 decurrent cells enlarged, oblong, thin-walled. Asexual brood bodies not seen. Sporophytes not known in Central America, description from Buck (1998). Setae elongate, reddish, smooth below, roughened below the capsule, 7–9 mm long. Capsules erect to suberect, cylindric, 0.8 mm long; exothecial cells around the mouth quadrate to oblate in 2–4 rows, dark, rectangular below, thin-walled, not collenchymatous; operculum and annulus not seen; peristome diplolepideous; exostome teeth whitish, erect when wet or dry, narrowly triangular, both surfaces papillose throughout, trabeculae weak at back; endostome pale, spiculose-papillose, basal membranes low, segments linear, lightly keeled, not perforate, cilia absent. Spores not seen. Calyptrae mitrate, reddish, irregularly lobed at base, naked, smooth, or slightly roughened above, more or less plicate.

Illustrations. Buck (1998, Pl. 16 9–14). Figure 145.
Habitat. On twigs by stream; 1900 m.
Distribution in Central America. HONDURAS. Lempira: *Allen 11914A* (MO).
World range: Central America; Caribbean.

Actinodontium pygmaeum is a small, slender species previously known only from the type specimen. Its yellowish green plants have erect stems with evenly foliate, linear-lanceolate leaves. As noted by Buck (1998), the upper leaf cells of *A. pygmaeum* are longer than those of *A. sprucei* (60–120 µm vs. 50–80 µm), but the two species are best distinguished by their leaf apices and plant size. Plants of *A. sprucei* are 10–20 mm high and have gradually acute to short-acuminate leaf apices, while those of *A. pygmaeum* are 5–7 mm high and have narrowly acuminate to subulate leaf apices. The Honduran collection of *A. pygmaeum* differs from that of the Dominican Republic in having somewhat larger plants with longer leaves (1.4–2.1 mm vs. 1.1–1.4 mm). In addition, the leaves in the Honduran collection are elimbate, with plane and consistently serrulate leaf apices, while their costae are never more than one-half the leaf length. In contrast, the leaves in the Dominican Republic specimen are not or scarcely bordered, narrowly recurved nearly throughout, subentire to serrulate above, and have costae 2/3–3/4 the leaf length. However, *Actinodontium* exhibits considerable variability in its leaves, as judged from the fact that *A. sprucei* has leaves in some collections with tightly recurved, more or less entire margins, while others have mostly plane margins that are distinctly serrulate. The only significant difference between the two collections appears to be in the length of their costae.

2. ***Actinodontium sprucei*** (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 325. 1877. *Lepidopilum sprucei* Mitt., J. Linn. Soc., Bot. 12: 370. 1869. Protologue. [Ecuador] Andes Quitenses, in sylva Canelos (3000 ped.), *Spruce*. Types. Mont. de Canelos, *Spruce* (NY, holotype); Canelos, 3000 ped., *Spruce* (NY, isotype).

Lepidopilum integrifolium Broth. *in* Urb., Symb. Antill. 3: 427. 1903. *Actinodontium integrifolium* (Broth. *in* Urb.) S. P. Churchill *in* W. R. Buck, Mem. New York Bot. Gard. 82: 49. 1998. Protologue. Hab. in Guade-

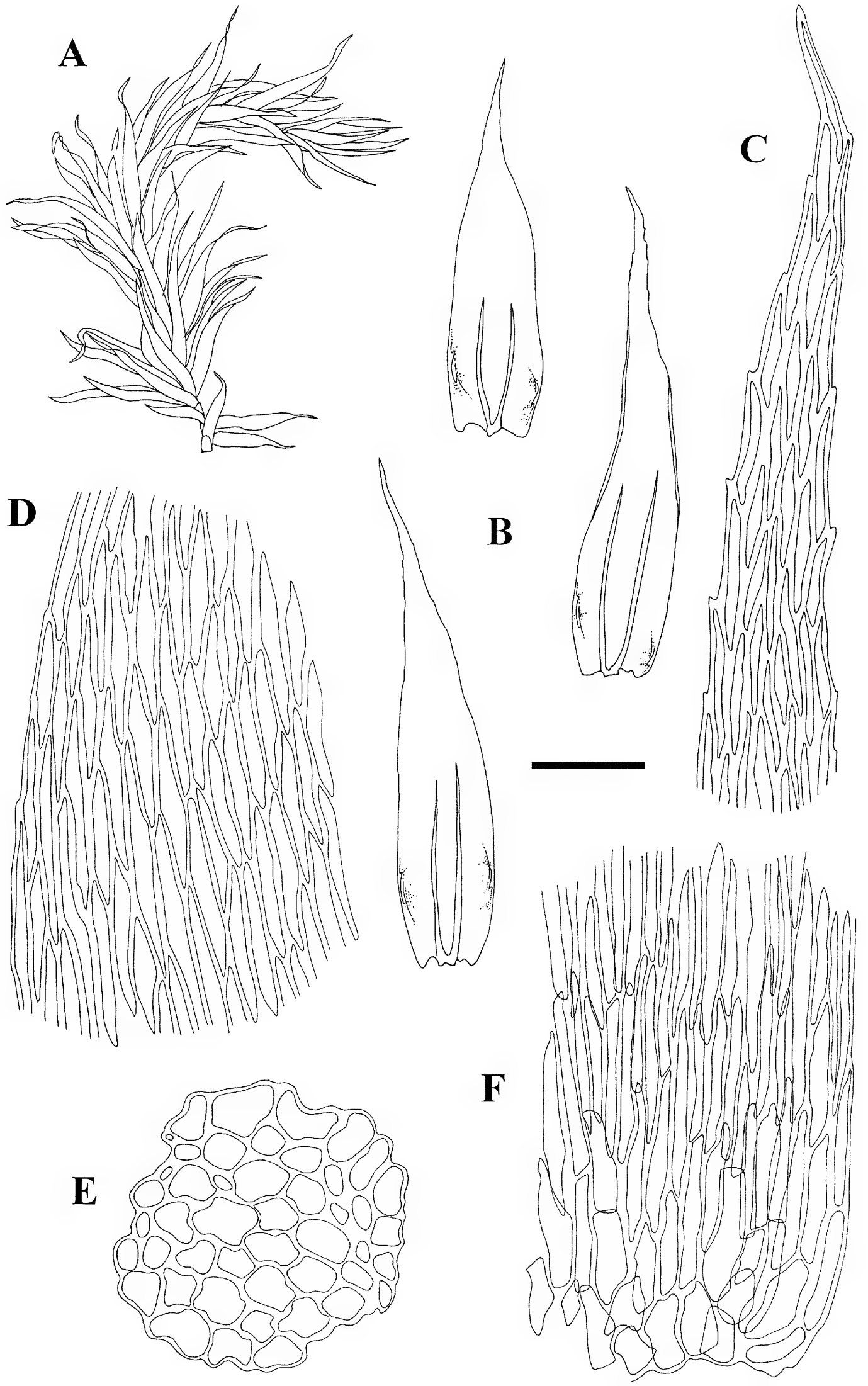
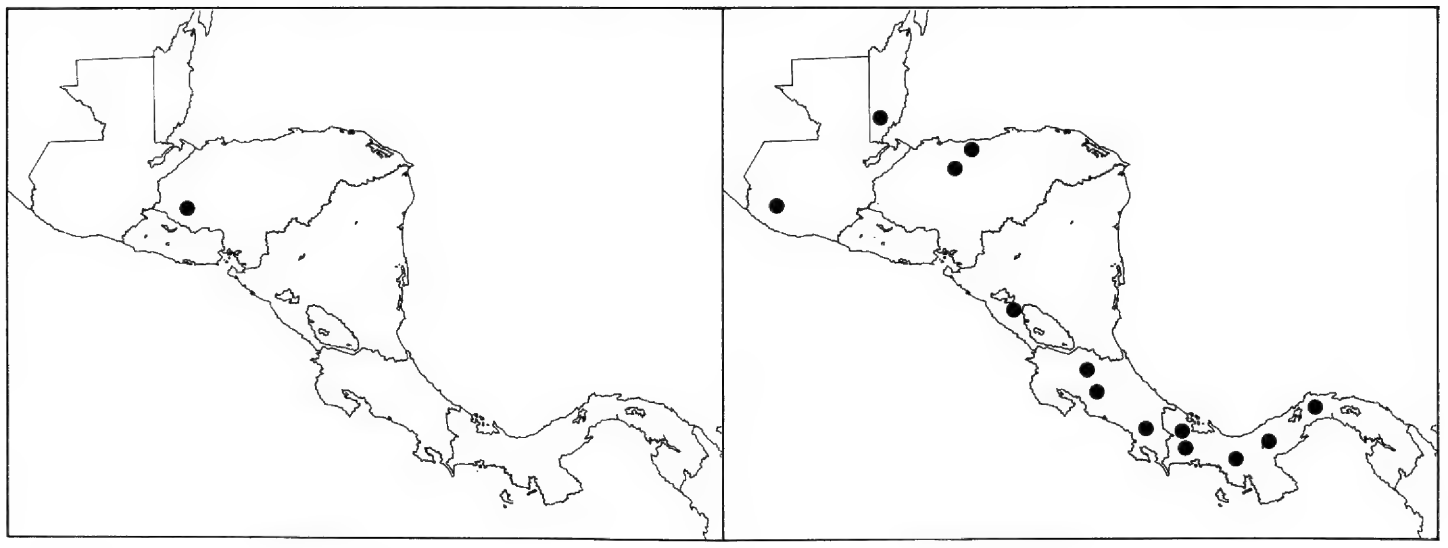


Figure 145. *Actinodontium pygmaeum*. A. Habit. B. Leaves. C. Leaf apex. D. Median leaf cells and margin. E. Stem in cross section. F. Basal and alar cells. Scale in mm: bar = 0.06 (C–F); bar = 0.5 (B); bar = 1.56 (A). All figure parts from *Allen 11914A*.



Actinodontium pygmaeum *Actinodontium sprucei*

loupe in Bois des Bains-Jaunes, ad truncos arborum rarior: *Duss n. 222* (in Herb. Berol.); Morne Grame-Verte: *Duss n. 460*[a] (in Herb. Berol.); Martinique in Morne-Rouge, ad truncos arborum: *Duss n. 372 ex p.* (in Herb. Berol.), *syn. nov.*

Actinodontium standleyi E. B. Bartram, Bryologist 49: 119. 1946. Protologue. Guatemala. Dept. Suchitepéquez; near Pueblo Nuevo, alt. about 700 m, *Standley 66941 in part.* Types. Guatemala. Dept. Suchitepéquez, near Pueblo Nuevo, alt. about 750 m, March 1, 1939, *Paul C. Standley 66941 in part* (FH, holotype; F, US, isotypes), *syn. nov.*

Actinodontium portoricense H. A. Crum & Steere, Bryologist 59: 252. 1956. Protologue. [Puerto Rico] On Sierra palm, trail running westward from El Toro ("Torito") to Ciénaga Alta, Sierra de Luquillo, *Steere 6458*, Feb. 10, 1940, TYPE (in herb. University of Michigan). Type. Puerto Rico, on sierra palm, trail running W. to to Ciénaga Alta, from El Toro, Sierra de Luquillo. Feb. 10, 1940, *Steere 6458* (NY, isotype), *syn. nov.*

Plants small to medium-sized, 10–20 mm long, yellowish green to golden reddish, in sparse (sometimes dense) tufts. Stems erect or ascending, not or sparsely branched, reddish, evenly or weakly complanate-foliate; stems in cross section with incomplete hyalodermis, subepidermis of 1–2 rows of smaller, thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2–3 cells long, basal 1–2 cells short-rectangular, reddish brown, upper 1–2 cells oblong-elongate, hyaline; rhizoids from scattered initials abaxial to the leaf insertions, roughened papillose, reddish brown, not or sparsely and irregularly branched. Leaves erect to erect-spreading when wet or dry, more or less symmetric, concave, oblong-lanceolate, 1.5–2.5 mm long, gradually acute to short-acuminate, decurrent; margins entire throughout or serrulate at the apex, narrowly recurved throughout or in the lower 3/4, indistinctly bordered by 1–2 rows of narrow, elongate cells; costae double, gradually divergent, 1/2–2/3 the leaf length; cells smooth, upper cells long-rhomboidal to long-hexagonal, 50–80 × 12–18 μm, firm-walled, lower cells longer and narrower, to 160 μm long; basal cells near insertions rectangular, reddish across the insertions; alar cells undifferentiated, 1–3 decurrent cells enlarged, oblong, thin-walled. Asexual reproduction by dense clusters of brood bodies borne in leaf axils, brood bodies uniseriate, 5–8-celled. Heteroicous or dioicous. Perigonia and perichaetia sessile along stems and branches. Setae elongate, 7–14 mm long, red to red brown, smooth or somewhat roughened below the capsule. Capsules erect, cylindric, neck moderately developed, 1.5–2.0 mm long; exothecial cells quadrate to shortly oblate at mouth, long-rectangular below, thick-walled, not collenchymatous; stomata rudimentary, on neck; opercula conic-rostrate, 0.5–0.7 mm long; annuli rudimentary, deciduous; peristome diplolepideous; exostome teeth white, erect to recurved when wet, incurved when dry (hydrocastique), narrowly triangular, both surfaces papillose throughout, dorsal trabeculae and median lines weak, ventral trabeculae moderately developed; endostome white, spiculose-papillose above, basal membranes low, segments linear, keeled, not or faintly perforate, cilia absent. Spores irregularly rounded to oval, 12–22 μm, lightly papillose. Calyptrae mitrate, red below, yellowish above, irregularly lobed at base, naked, smooth, 1.5–2.0 mm long.

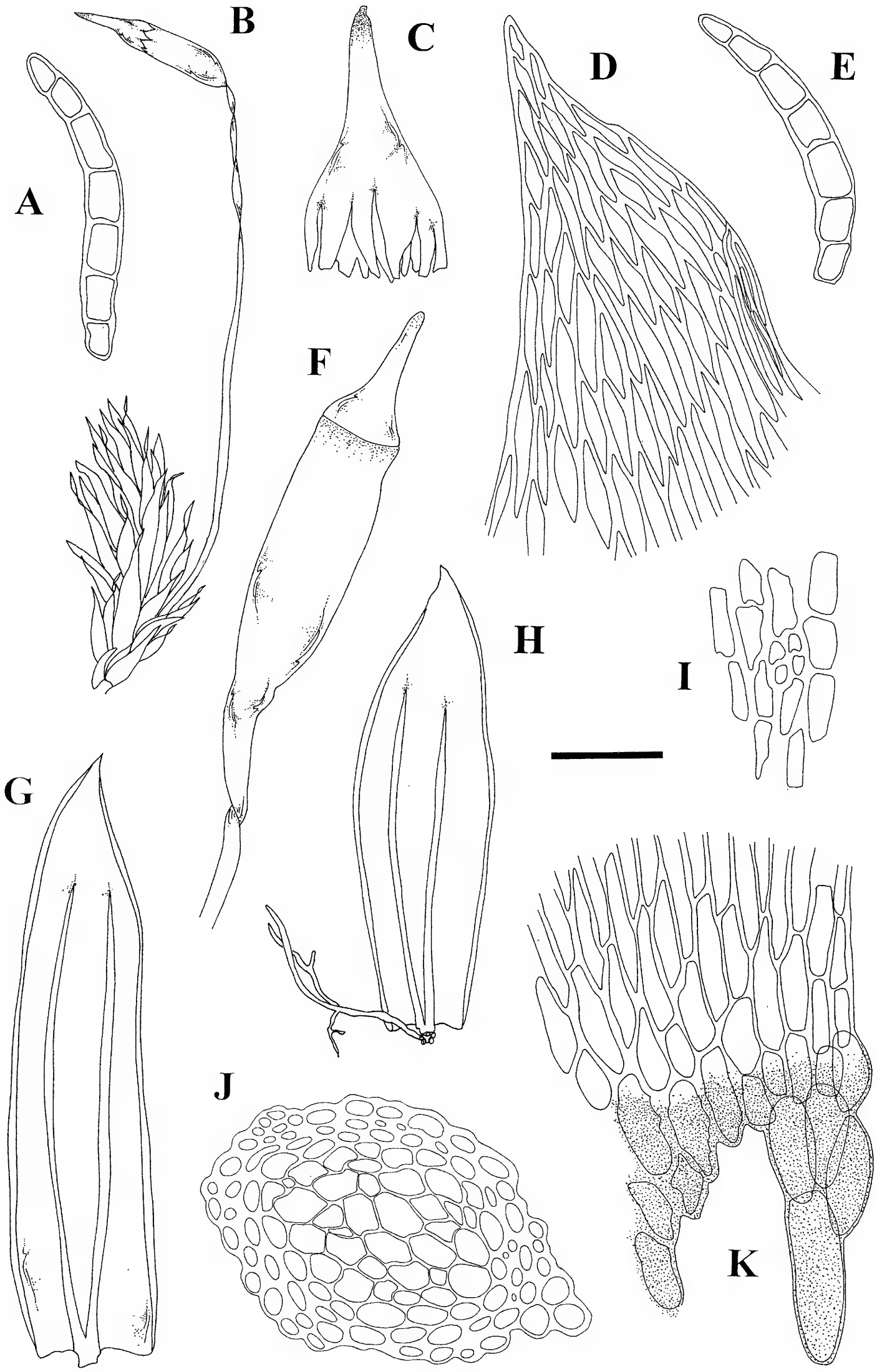


Figure 146. *Actinodontium sprucei*. A & E. Gemmae. B. Habit with sporophyte. C. Calyptra. D. Leaf apex. F. Seta, capsule, and operculum. G & H. Leaves. I. Stoma. J. Stem in cross section. K. Basal and alar cells. Scale in mm: bar = 0.06 (D, I, K); bar = 0.05 (A, E); bar = 0.08 (J); bar = 0.5 (F–H); bar = 0.6 (C); bar = 2.0 (B). A, E, H from *Allen 17348*; B, G from *Lyon 352*; C, F, I from *Crosby 10134*; D from *Spruce* (type); all other figure parts from *Nee 11257*.

Illustrations. Bartram (1949, Fig. 137 D–F); Welch (1971b, Figs. 1–15); Welch (1972a, Figs. 1–14); Welch (1974, Figs. 1–8); Sharp *et al.* (1994, Fig. 618); Churchill and Linares (1995, Fig. 32 a–h); Buck (1998, Pl. 18 1–5); Gradstein *et al.* (2001, Fig. 163 A–D); Buck (2003, Fig. 84). Figure 146.

Habitat. On fallen and rotting branches, tree or palm trunks, twigs, and thatched roofs; 300–2000 m.

Distribution in Central America. BELIZE. Toledo: *Allen 19021* (MO). GUATEMALA. Suchitepéquez: *Standley 66941* (F, FH, US). HONDURAS. Atlántida: *Allen 17348* (MO); Yoro: *Allen 13565A* (MO). NICARAGUA. Granada: *Granzow de la Cerda & Moreno GC-1512* (DUKE, MO). COSTA RICA. Alajuela: *Crosby & Crosby 5903* (MO); Puntarenas: *Dauphin 1994* (MO); San José: *Crosby 13126* (MO). PANAMA. Bocas del Toro: *Allen 5587* (MO); Chiriquí: *Allen 4992* (MO); Coclé: *Croat 67274* (MO); Panamá: *McPherson 7414A* (MO); Veraguas: *Nee 11257* (MO, NY, PMA).

World range: Mexico; Central America; Caribbean; Western and Northern South America.

Actinodontium sprucei is extremely variable in size and often grows in sparse tufts. Its plants have erect stems that are not or weakly branched. They are typically yellowish green in color, but are also often bronze to reddish tinted. The oblong-lanceolate leaves are concave and usually evenly foliate, although some plants can be obscurely complanate. The weakly bordered leaf margins in *A. sprucei* are narrowly revolute, sometimes nearly throughout, and entire to serrulate at the acute to short-acuminate apex. Although the alar cells are undeveloped, the leaves are decurrent by 1–3 enlarged, bulging, rounded to oval cells. In cross section the stems appear to have a discontinuous hyalodermis; however, this structure may actually represent enlarged decurrent cells rather than a true hyalodermis. The leaf cells are long-rhomboidal, quite variable in width, and firm-walled throughout. *Actinodontium sprucei* has elongate, mostly smooth setae and erect-cylindric capsules with rudimentary stomata. The peristome is whitish, papillose throughout, and strongly hygrocastique, *i.e.*, exostome teeth spreading outward when wet.

Actinodontium sprucei is usually separated from *A. integrifolium* by its shorter, narrower leaves that are more distinctly acuminate. The two taxa, however, are extremely variable in leaf form and marginal serration, not only between but also within populations. Furthermore, *A. standleyi* represents an intermediate form that completely bridges the gap between *A. sprucei* and *A. integrifolium*. There are two collections on the type sheet of *A. sprucei*. One, annotated as the holotype, represents the typical expression of the species in which the margins are tightly recurved and more or less entire. The other, an isotype, has leaves with mostly plane margins that are distinctly serrulate.

Most species of *Lepidopilum* differ from *Actinodontium sprucei* in having creeping primary stems and strongly complanate leaves. However, there is a *Lepidopilum* group (centered on *L. longifolium*) with weakly complanate leaves that is extremely similar in plant aspect. *Lepidopilum longifolium* differs from *A. sprucei* in having leaves with longer, more narrowly acuminate apices, more weakly recurved leaf margins, and shorter costae. These distinctions, though, can be difficult to apply without the benefit of comparative material or previous experience with the species. The sporophytes of *L. longifolium*, however, have hispid setae, and the calyptrae have multiseriate hairs.

2. *Amblytropis* (Mitt.) Broth., Nat. Pflanzenfam. I(3): 953. 1907. *Hookeria* Sm. sect. *Amblytropis* Mitt., J. Linn. Soc., Bot. 12: 339. 1869.

Plants small to medium-sized, pale greenish, yellowish green, to red, in mats. Stems prostrate, irregularly branched, yellowish, becoming reddish with age, somewhat complanate-foliate; stems in cross section when old with a 1-stratose hyalodermis, subepidermis of 1–2 rows of smaller, thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs fugacious, 2 cells long, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids sparse, from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect to laxly imbricate, weakly crispate when dry, erect to erect-spreading when wet, lateral leaves somewhat asymmetric, concave, oblong to broadly ovate, constricted at about 3/4 the leaf length, gradually acute to narrowly acuminate, apiculate, ventral and dorsal leaves symmetric, ovate, not constricted, acute, leaves not decurrent; margins entire or obscurely serrate, bordered by 1–2 rows of narrow, rectangular cells, plane; costae double, weak, 2 cells thick, gradually divergent, 1/2–2/3 the leaf length; cells

smooth, upper and median cells broadly hexagonal to elongate-hexagonal, laxly bulging; basal cells oblong-rectangular to long-rectangular; alar cells undifferentiated. Asexual reproduction sometimes by fragile leaf apices. Dioicous [and autoicous ?]. Male plants smaller, more slender than female plants. Perigonia and perichaetia sessile along stems and branches. Setae elongate, spinose to hispid. Capsules suberect to inclined, ovoid, neck moderately developed; exothecial cells in 2–3 rows, reddish, quadrate to shortly oblate at mouth, yellowish, long-rectangular below, thick-walled, not collenchymatous; stomata rudimentary, on neck; opercula conic to conic-rostrate; annuli rudimentary, deciduous; peristome diplolepideous; exostome teeth erect to recurved when wet, incurved when dry (hydrocastique), narrowly triangular, papillose throughout on both sides, dorsal (outer) surface light yellow, ventral side dark red and about 1/2 as broad as the dorsal surface, dorsal trabeculae and median lines weak, ventral trabeculae moderately developed; endostome as long as the exostome, yellowish red, papillose throughout, basal membranes high, segments broad, weakly keeled, not or faintly perforate, cilia rudimentary. Calyptrae mitrate, irregularly and narrowly lobed at base, sparsely hairy, sometimes with persistent archegonia.

Amblytropis is a genus of four species restricted to Central America and western South America. There is only one species of the genus (*A. hispidula*) in Central America. Plants of *Amblytropis* usually occur in mats on tree trunks or rotting logs. They have a pale green color and are sometimes purplish red tinged. The gametophytes and sporophytes of *Amblytropis*, as too often encountered in members of the Hookeriaceae, indicate dramatically different generic relationships. The gametophytes have prostrate stems with erect, somewhat complanate leaves that are somewhat crisped when dry. Older stems have a hyalodermis, and their rhizoids are relatively sparse, arising from rhizoidal initials (on stems or branches that touch the substrate) immediately abaxial to the leaf insertions. The ovate to oblong leaves are distinctly constricted in the upper part and have plane margins. The plants have an aspect similar to species of *Brymela* or *Thamniopsis*, but the leaves have a net-like areolation, faint but long double costae, and a border that all are identical in form to those of many *Cyclodictyon* species. However, the sporophytes have densely spinose to hispid setae, completely papillose exostome teeth with narrow ventral plates, and long, broad, unperforate to weakly perforate endostomial segments identical to those found in many *Lepidopilum* species. Additional noteworthy features of *Amblytropis* include the presence in one species of leaves with fragile, deciduous apices, strongly hygrocastique peristome, and rudimentary stomata.

In Central America *Amblytropis* is distinguished from all members of the Hookeriaceae by its odd combination of a *Cyclodictyon*-like gametophyte and a *Lepidopilum* sporophyte. Collections that lack sporophytes can be recognized as *Amblytropis* by its leaves that are distinctly constricted at about two-thirds of the way from the base.

The name *Amblytropis* combines the Greek *amblys* (blunt, obtuse, dull) and *tropis* (keel or ridge) for reasons that are not readily apparent, but may refer to its broad, weakly keeled endostomial segments.

1. Upper leaf margins consistently serrate to serrulate 2
1. Upper leaf margins entire or occasionally obscurely serrulate 3

2. Leaves oblong-lanceolate, 0.4–0.6 mm wide at widest point . . . . . [*A. setosa*]
2. Leaves ovate-lanceolate, 0.8–0.9 mm wide at widest point . . . . . [*A. ovata*]

3. Plants pale green, usually reddish tinged; leaves weakly crispate when dry; leaf borders weakly developed, obscure; apices broadly acute . . . . . *A. hispidula*
3. Plants green to yellowish green; leaves strongly crispate to undulate when dry; leaf borders well developed, of 2–4 rows of narrow, elongate cells; apices acuminate . . . . . [*A. gemmacea*]

Amblytropis hispidula (Mitt.) Broth., Nat. Pflanzenfam. I(3): 954. 1907. *Hookeria hispidula* Mitt., J. Linn. Soc., Bot. 12: 339. 1869. Protologue. [Colombia] Nova Granata, *Purdie*.

Cyclodictyon jamesonii H. Rob., Phytologia 21: 4. 1971. Protologue. [Costa Rica] Puntarenas: Near Monteverde, forest, 4300 ft., *W. James 1969-44*. Type. Forests, 4300 ft. elev. Near Monteverde, Costa Rica, Feb. 1969, *Walter James 1969-44* (US, holotype; NY, isotype).

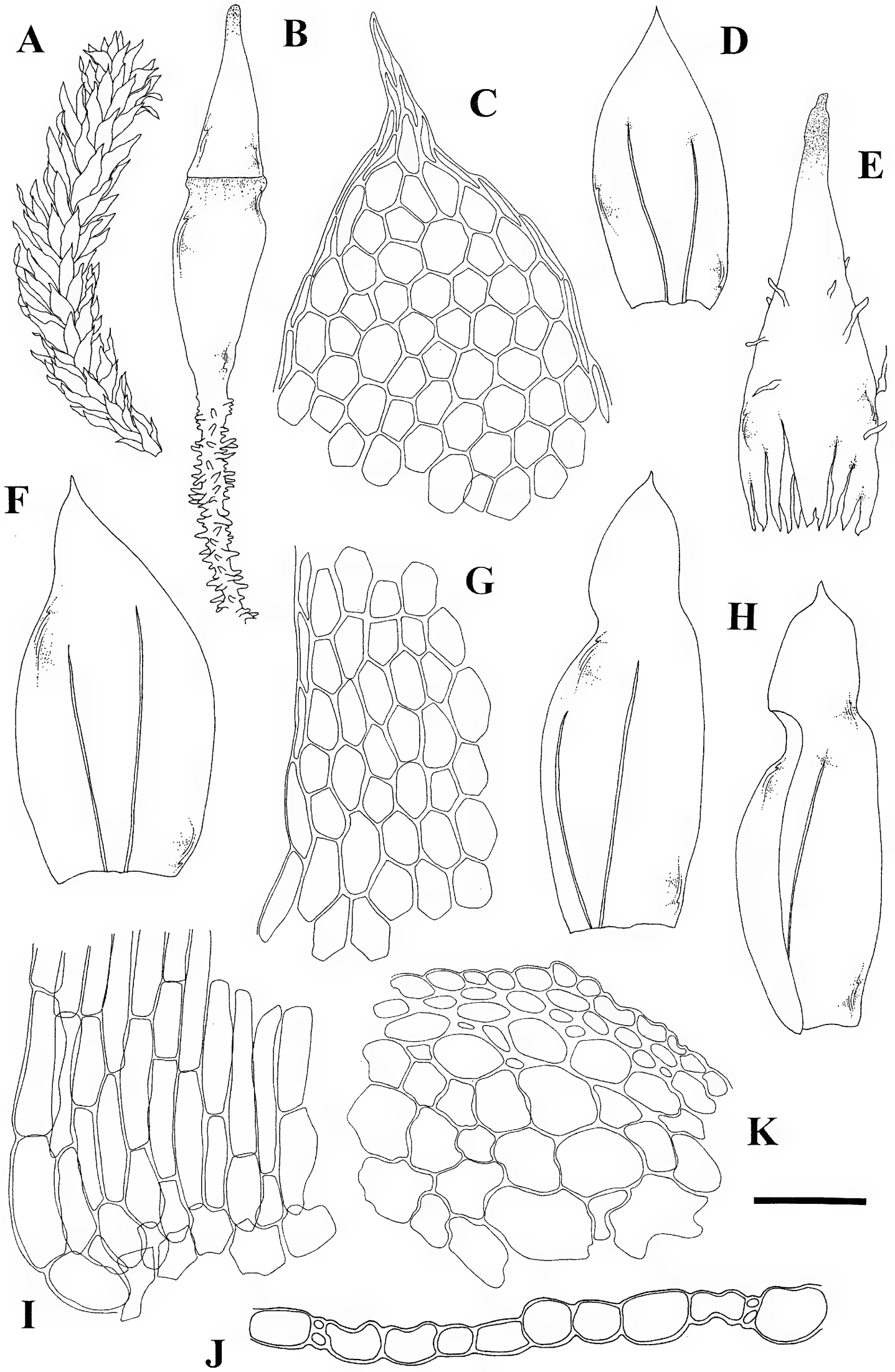
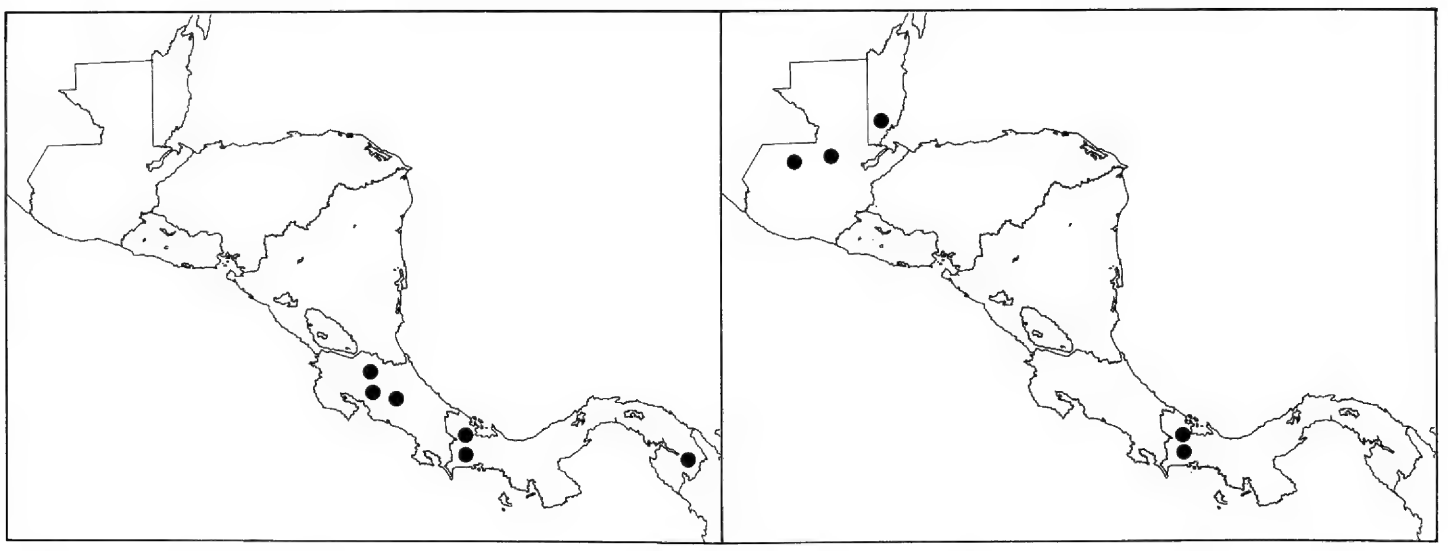


Figure 147. *Amblytropis hispidula*. A. Habit. B. Operculum, capsule, and upper part of seta. C. Leaf apex. D. Ventral leaf. E. Calyptra. F. Dorsal leaf. G. Upper median leaf cells and margin. H. Lateral leaves. I. Basal and alar cells. J. Cross section of costa at midleaf. K. Stem in cross section. Scale in mm: bar = 0.05 (J); bar = 0.08 (C, G, I, K); bar = 0.5 (B, D, F, H); bar = 0.6 (E); bar = 2.5 (A). All figure parts from *Allen 5500*.



Amblytropis hispidula *Brymela angustiretis*

Plants small to medium-sized, 1–3 cm long, pale greenish, yellowish green to red, in dense mats. Stems prostrate, irregularly branched, yellowish, becoming reddish with age, somewhat complanate-foliate; stems in cross section when young with all cells homogeneously thin-walled, when old with a 1-stratose hyalodermis, subepidermis of 1–2 rows of smaller, thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs fugacious, 2 cells long, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids sparse, from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect to laxly imbricate, weakly crispate when dry, erect to erect-spreading when wet, lateral leaves somewhat asymmetric, concave, oblong to broadly ovate, 2.0–2.5 mm long, constricted at about 3/4 the leaf length, gradually acute, narrowly apiculate, ventral and dorsal leaves symmetric, ovate, not constricted, acute, not decurrent; margins entire throughout, occasionally obscurely serrulate, indistinctly bordered by 1 row of narrow, rectangular cells, plane; costae double, weak, 2 cells thick, gradually divergent, 1/2–2/3 the leaf length; cells smooth, upper and median cells broadly hexagonal to elongate-hexagonal, laxly bulging; basal cells oblong-rectangular to long-rectangular, 70–130 × 20–25 µm; alar cells undifferentiated. Asexual reproduction by fragile leaf apices. Dioicous. Male plants smaller, more slender than female plants. Perigonia and perichaetia sessile along stems and branches. Setae elongate, 10–18 mm long, yellow when young, becoming red to red brown when old, spinose to hispid. Capsules suberect to inclined, ovoid, neck moderately developed, 1.0–1.5 mm long; exothecial cells at mouth reddish, quadrate to shortly oblate in 2–3 rows, yellowish, long-rectangular below, thick-walled, not collenchymatous; stomata rudimentary, on neck; opercula conic to conic-rostrate, 1.0 mm long; annuli rudimentary, deciduous; peristome diplolepideous; exostome teeth erect to recurved when wet, incurved when dry (hydrocastique), narrowly triangular, papillose throughout on both sides, dorsal (outer) surface light yellow, ventral side dark red and about 1/2 as broad as the dorsal surface, dorsal trabeculae and median lines weak, ventral trabeculae moderately developed; endostome as long as the exostome, yellowish red, papillose throughout, basal membranes high, segments broad, weakly keeled, not or faintly perforate, cilia rudimentary. Spores irregularly rounded to oval, 10–16 µm, faintly papillose. Calyptrae mitrate, red above, yellowish below, irregularly and narrowly lobed at base, sparsely hairy, sometimes with persistent archegonia, 3.0 mm long.

Illustrations. Robinson (1971a, Figs. 1–3); Churchill and Linares (1995, Fig. 33 a–e); Gradstein *et al.* (2001, Fig. 163 F–I). Figure 147.

Habitat. On tree trunks; 950–1600 m.

Distribution in Central America. COSTA RICA. Alajuela: *Lyon 54* (CR, MO); Cartago: *Engel 8377* (CR, F, MO); San José: *Holz & Schäfer-Verwimp CR 99-1315* (MO). PANAMA. Bocas del Toro: *Allen 5626* (MO); Chiriquí: *Allen 5500* (H, MO, NY, PMA, S); Darién: *Folsom 4467* (MO, PMA).

World range: Central America; Western South America.

Amblytropis hispidula is a medium-sized species found on tree trunks (especially palms) in Costa Rica and Panama. The plants have laxly erect, somewhat complanate, crisped leaves when dry, and although they are typically pale green in color, exposed parts of the plants are tinged purplish red. The young stems of *A. hispidula* in cross section consist of thin-walled cells that are somewhat smaller toward the outside but otherwise undifferentiated. As they age, however, the stems develop 1–2 rows of small, thick-walled cells below the surface layer cells, and as a result a hyalodermis is demarcated. The gametophytes of *A. hispidula* have an aspect similar to species of *Brymela* or *Thamniopsis*, but the leaves have a net-like areolation, faint but long, double costae, and a weak border that is identical to the gametophytes of many *Cyclodictyon* species. However, the sporophytes have densely spinose to hispid setae, completely papillose exostome teeth with narrow ventral plates, and long, broad, unperforate to weakly perforate endostomial segments identical to those found in many *Lepidopilum* species. Plants of *A. hispidula* with sporophytes are readily recognizable because of this odd combination of gametophytic and sporophytic characters. *Amblytropis hispidula* is dioicous; nevertheless, plants without sporophytes can be recognized by examining the upper portions of the lateral leaves. These leaves are distinctly constricted at about two-thirds of the way from the base. The constriction coincides with a zone of weakness in the cells. As a result the leaf apices are fragile and often deciduous.

Amblytropis setosa is a northern South American species present in Colombia. It differs from *A. hispidula* in having leaves with better-developed upper borders and consistently serrate to serrulate margins. The leaves of *A. setosa* are similar to those of *A. hispidula* in being constricted above; however, the constriction does not appear to be associated with a zone of weakened cells and the leaf apices are not fragile. Furthermore, in *A. setosa* the leaf apices above the constrictions are narrowly acuminate, while those of *A. hispidula* are broadly acute.

3. *Brymela* Crosby & B. H. Allen, Monogr. Syst. Bot. Missouri Bot. Gard. 11: 211. 1985.

Plants small, medium-sized, or robust, green, yellowish green, yellowish red, or red, in thin or dense mats. Stems prostrate, irregularly branched, hyaline to yellowish when young, becoming reddish with age, complanate-foliate or evenly foliate; stems in cross section with 2–5-stratose sclerodermis, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2–4 cells long, basal 1–3 cells short-rectangular, reddish brown, upper 1–2 cells oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect, erect-incurved, falcate-secund, or flattened, at times twisted, often rugose when dry, erect-spreading when wet, symmetric or weakly asymmetric, concave, ovate, ovate-lanceolate, oblong-lanceolate to lanceolate, or oblong-ovate, rounded, obtuse, acuminate to long-acuminate; margins denticulate, serrate, or sinuate above, serrulate, subentire, or entire below, plane or narrowly recurved above, at times broadly incurved on one side below; costae double, thin or thick, ending 2/3–3/4 the leaf length, diverging throughout, smooth on back, at times projecting at the tips; cells smooth or prorate, upper cells rhomboidal, long-rectangular to linear-flexuose, firm-walled; basal cells near the insertions oblong-rectangular to long-rectangular, often porose; alar cells undifferentiated. Dioicous. Setae elongate, smooth or smooth below, roughly papillose to tuberculate on capsule necks and upper parts of setae. Capsules inclined, symmetric and cylindric, neck well developed; exothecial cells oblong to rounded-rectangular, incrassate, more or less collenchymatous; rudimentary 2–6-celled stomata on neck; opercula long-rostrate, conic at base; annuli massive, persistent, of 4–8 rows of yellowish, hexagonal cells; peristome diplolepideous; exostome teeth narrowly triangular, with broad median furrows, densely and closely striate below, coarsely papillose above, ventral surface hyaline to yellowish, smooth to lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, cilia absent or rudimentary. Calyptrae mitrate, irregularly lobed, reddish and lightly roughened, yellowish below.

Brymela is a Neotropical genus restricted to Central America, the Caribbean, and northwestern South America. The genus was originally described for a single, especially robust, epiphytic moss from western Panama. Buck (1987) considerably expanded its generic concept when he transferred nine species of *Hookeriopsis* into *Brymela.* One of these transfers (*H. callicostelloides*) is better

placed in *Callicostella.* The present treatment adds four more species to *Brymela*, bringing the total number of species in the genus to thirteen. Plants of *Brymela* are often reddish in color. Its stems have a sclerodermis and no pseudoparaphyllia. The leaves of *Brymela* are nearly always undulate to rugose when dry and have serrate to serrulate or subentire, non-bordered margins. The leaf costae are thin or thick, usually diverge throughout, are smooth on dorsal surface, and only sometimes weakly project at the tips. The leaves of *Brymela* have a homogenous areolation, with usually elongate, firm- or thick-walled and porose cells. The capsules of *Brymela* are distinctive in having a massive, persistent annulus consisting of 4–6 rows of yellowish, hexagonal cells. As in other members of the Hookeriaceae, the rudimentary stomata are composed of 2–6 cells.

Brymela can be confused with the other *Hookeriopsis* segregates: *Hookeriopsis*, *Thamniopsis*, and *Trachyxiphium. Hookeriopsis* and *Brymela* are similar in lacking a stem hyalodermis and in having similarly shaped, elimbate leaves. In both genera the cells are elongate, firm- to thick-walled, and homogeneous throughout. *Hookeriopsis* differs from *Brymela* only in having weak costae that barely extend above midleaf. *Thamniopsis* is an extremely troublesome genus, with species that often have strongly dimorphic leaves. It is similar to *Brymela* in size, and both genera often have undulate or rugose leaves. *Thamniopsis* differs from *Brymela* in having a well-developed stem hyalodermis. Furthermore, the leaf margins in *Thamniopsis* are strongly toothed (often by swollen, bifid teeth) and bordered by elongate cells. Lastly, the costae in *Thamniopsis* are often spined, or even crested, and the leaves have a heterogeneous areolation: upper cells usually short and firm-walled, basal cells elongate, enlarged, bulging, and thin-walled. *Trachyxiphium* and *Brymela* both lack a stem hyalodermis, and their leaves have a homogeneous areolation. Typically, the leaf cells in *Trachyxiphium* have thinner cell walls than those of *Brymela*, the leaf margins have swollen, often bifid teeth, and the costae are strong, spined, often crested, with paired, bifid teeth.

The name *Brymela* is an anagram based on the name of the collector of the type species, Barry Hammel.

1. Primary stems strongly creeping, secondary stems short, mostly unbranched; plants strongly complanate-foliate when dry; leaves plane . . . . . 2. *B. complanata*
1. Primary stems weakly creeping, secondary stems long, irregularly branched; plants evenly foliate or weakly complanate-foliate when dry; leaves undulate, rugose or plicate (except *B. crosbyi*) 2

2. Leaf apices acute to rounded-obtuse . . . . . 5. *B. obtusifolia*
2. Leaf apices acuminate 3

3. Plants robust, stems to 11 cm long; leaves 6–8 mm long . . . . . 6. *B. tutezona*
3. Plants slender to medium-sized, stems to 3 cm; leaves 1–2 mm long 4

4. Leaves abruptly constricted at base of acumina ; upper leaf cells 14–40 µm long . . . . . 4. *B. laevinervis*
4. Leaves gradually acuminate; upper leaf cells 20–70 µm long 5

5. Leaves plicate; plants with gemmiferous branches and terminal clusters of gemmae . . . . . 3. *B. crosbyi*
5. Leaves usually undulate; plants lacking gemmiferous branches or gemmae 6

6. Leaves falcate, lanceolate to narrowly ovate-lanceolate, long, narrowly acuminate; costae often ending on or very near the upper margins, often shortly projecting at the tips . . . . . 7. *B. websteri*
6. Leaves straight, ovate-lanceolate, shortly acuminate; costae ending in the lamina well away from the margins, not projecting at the tips . . . . . 1. *B. angustiretis*

1. *Brymela angustiretis* (E. B. Bartram) B. H. Allen, *comb. nov. Hookeriopsis angustiretis* E. B. Bartram, Bryologist 49: 119. 1946. Protologue. Guatemala. Dept. Alta Verapaz: Montaña Yxocubvain, 2 1/2 miles west of Cubilgüitz, alt. 300–500 m, *Steyermark 44970*. Type. Guatemala. Dept. Alta Verapaz: Montaña Yxocubvain, 2 1/2 miles west of Cubilgüitz, alt. 300–500 m, March 12, 1942, *Julian A. Steyermark 44970* (FH, holotype).

Plants small to medium-sized, 1–3 cm long, green or yellowish red, occasionally pale greenish, in thin or dense glossy mats. Stems prostrate, irregularly branched, hyaline to yellowish when young,

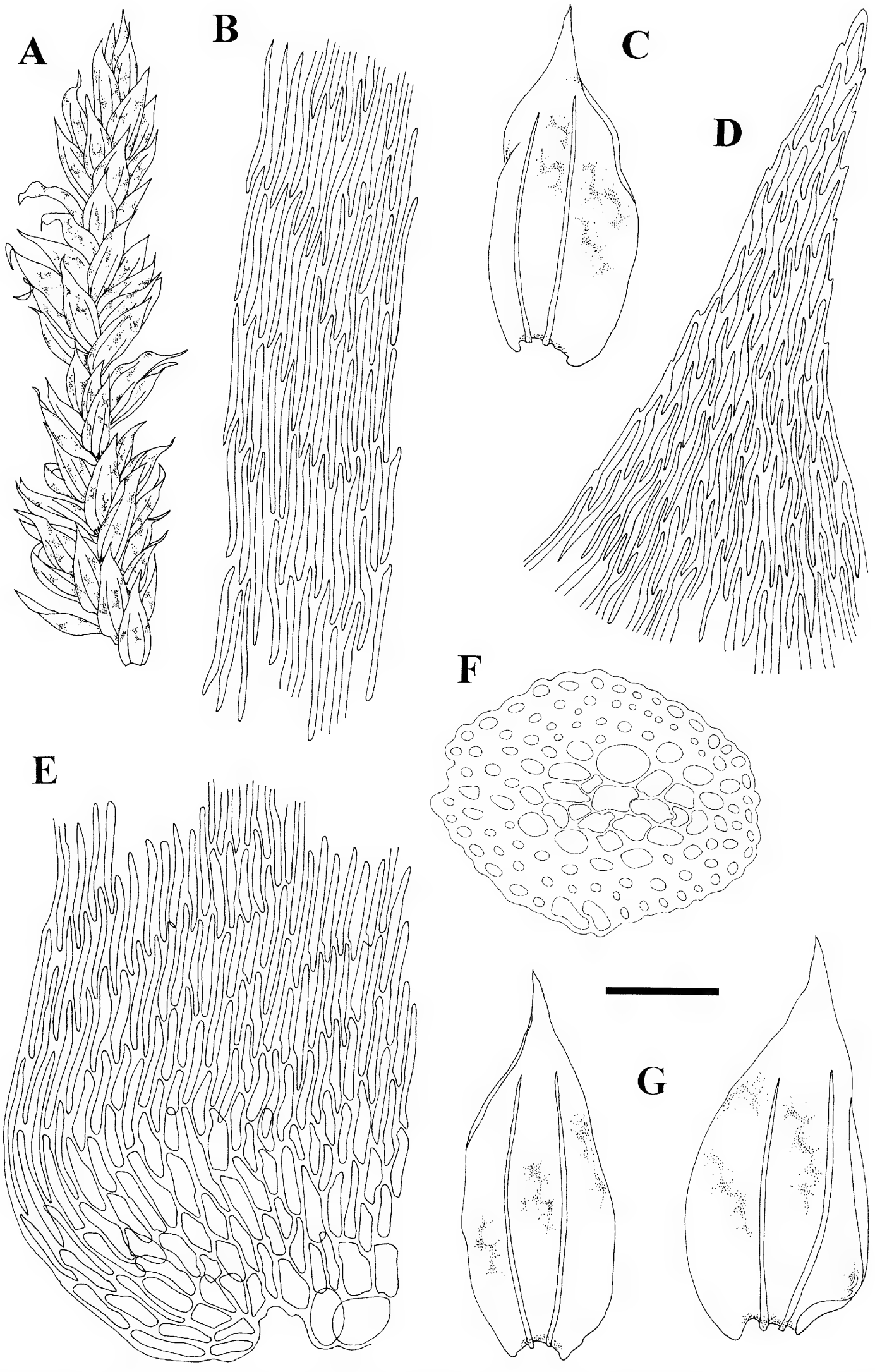


Figure 148. *Brymela angustiretis*. A. Habit. B. Median leaf cells. C & G. Leaves. D. Leaf apex. E. Basal and alar cells. F. Stem in cross section. Scale in mm: bar = 0.05 (B, D, E); bar = 0.08 (F); bar = 0.4 (C, G); bar = 1.56 (A). B, C from *Steyermark 44970* (type); all other figure parts from *Allen 18869*.

becoming reddish with age, somewhat complanate-foliate or evenly foliate; stems in cross section with sclerodermis of 2–3 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2–3 cells long, basal cell short-rectangular, reddish brown, upper 1–2 cells oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves somewhat flattened and variably undulate when dry, erect-spreading when wet, symmetric or weakly asymmetric, concave, ovate-lanceolate, acuminate, 1.2–1.6 mm long; margins denticulate above, entire below, plane or narrowly recurved above; costae double, thin, faint, ending 3/4 the leaf length, diverging throughout, smooth on back, not projecting at the apex; cells smooth, upper cells linear-flexuose, 30–70 × 3–4 μm, firm-walled, cells between the costae shorter than cells near the margins; basal cells near the insertions oblong-rectangular to long-rectangular, often porose; alar cells undifferentiated. Dioicous (?). Sporophytes unknown.

Illustrations. Bartram (1949, Fig. 136 D–F). Figure 148.

Habitat. On vertical bluffs, seeping cliffs and ledges, rocks near and in streams, roots, vines, or decomposing trunks; 300–1737 m.

Distribution in Central America. BELIZE. Toledo: *Allen 18545* (BRH, MO). GUATEMALA. Alta Verapaz: *Steyermark 44970* (FH); Quiché: *Sharp 2405a* (FH, NY, TENN). PANAMA. Bocas del Toro: *McPherson 8850H* (MO); Chiriquí: *Salazar et al. 4884* (MO).

World range: Central America.

Brymela angustiretis is a small to medium-sized species with irregularly branched stems and more or less complanate leaves that can be distinctly rugose when dry. Its ovate-lanceolate leaves are gradually acuminate and its firm-walled leaf cells are linear-flexuose. The costae of *B. angustiretis* are a distinctive feature of the species: thin, often faint, ending well below the apex, smooth at back, not ending in a projecting point.

In Central America *B. angustiretis* can be confused with *B. laevinervis* and *B. websteri*, because all three have ovate-lanceolate, rugose leaves with thin costae that are smooth at back and do not or faintly project at the tips. *Brymela laevinervis* differs from *B. angustiretis* in having leaves that are abruptly constricted at the base of the acumen and much shorter leaf cells (14–40 μm vs. 30–70 μm). *Brymela websteri* differs from *B. angustiretis* in having narrower, falcate-secund leaves that are long and narrowly acuminate. The costae in *B. websteri* also differ from those of *B. angustiretis* in being longer and usually more or less merging or ending very near the upper margins.

2. *Brymela complanata* B. H. Allen, *sp. nov.* Type. Panama. Colón: 1–2 hours walk along path beginning at end of Santa Rita Ridge Road, which terminates 17.1 km after leaving Boyd-Roosevelt Highway, 620 m, 9°15′N, 79°40′W, 22–23 May 1975, *Marshall R. Crosby 10386* (MO, holotype; NY, PMA, isotypes).

Species haec a *B. fissidentoide* foliis parvioribus differt.

Plants small, green to yellowish green, occasionally yellowish red, in loose, glossy mats. Primary stems creeping, to 6.5 cm long, secondary stems erect to 1 cm long, sparsely and irregularly branched, yellowish when young, becoming reddish with age, complanate-foliate; stems in cross section with epidermis of 2–4 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2–3 cells long, basal 1–2 cells short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from dense clusters of initials abaxial to the primary stem leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves somewhat erect, flattened, not undulate when wet or dry, primary stem leaves triangular-lanceolate to broadly ovate-lanceolate, 0.9–1.2 mm long; secondary stem leaves ovate-lanceolate to lanceolate, 1.0–1.3 mm long, broadly acuminate; margins serrulate above, subentire below, broadly incurved on one side below, plane to erect above, rounded at base; costae double, thin, ending 3/4 the leaf length, more or less parallel above the base, one branch often longer than the other, smooth on back, not or weakly projecting at the tips; cells smooth, firm- to thick-walled, upper cells long-rectangular to linear, at times flexuose, usually porose, 18–40 × 3–4 μm, median cells and basal

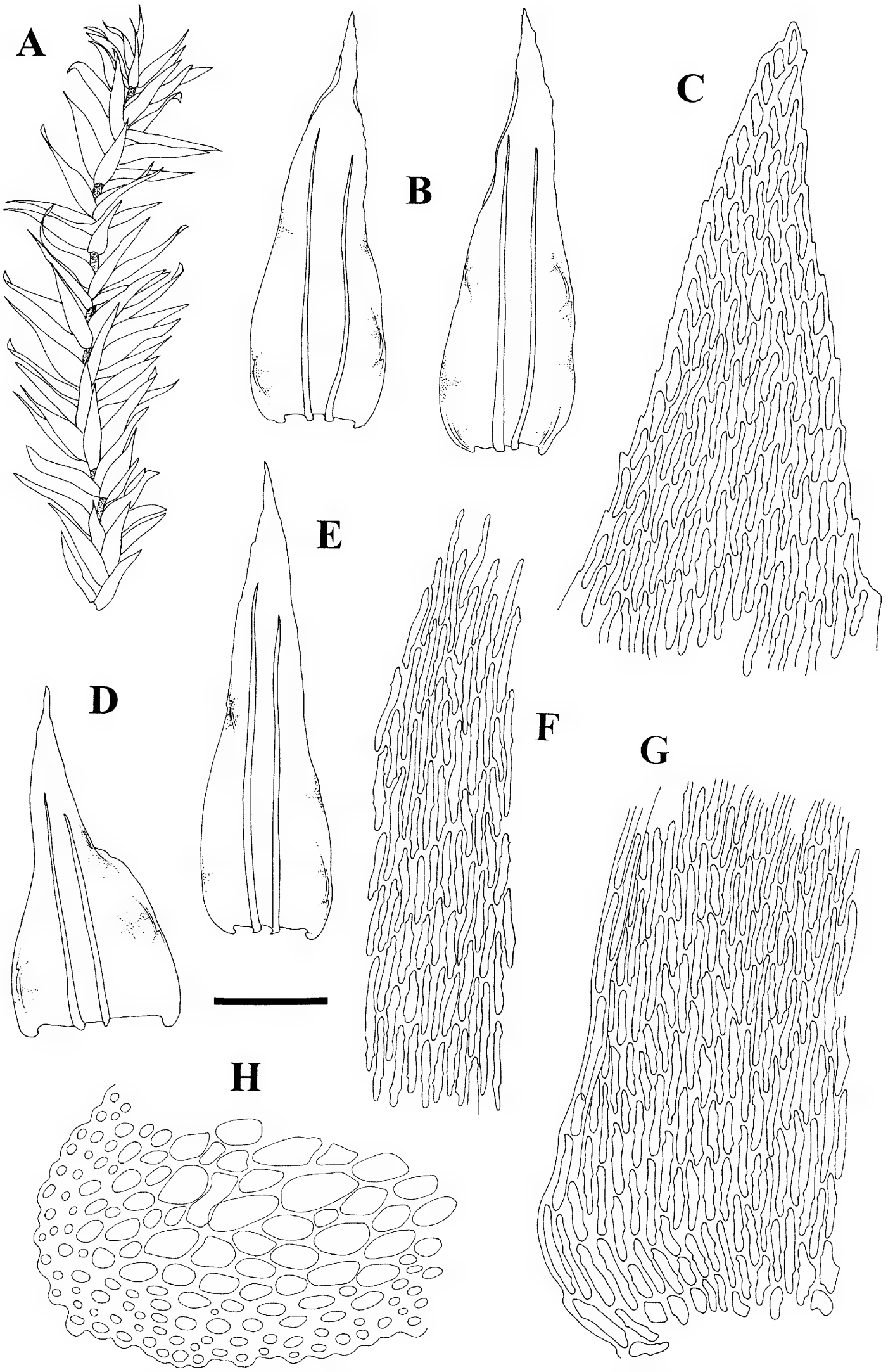
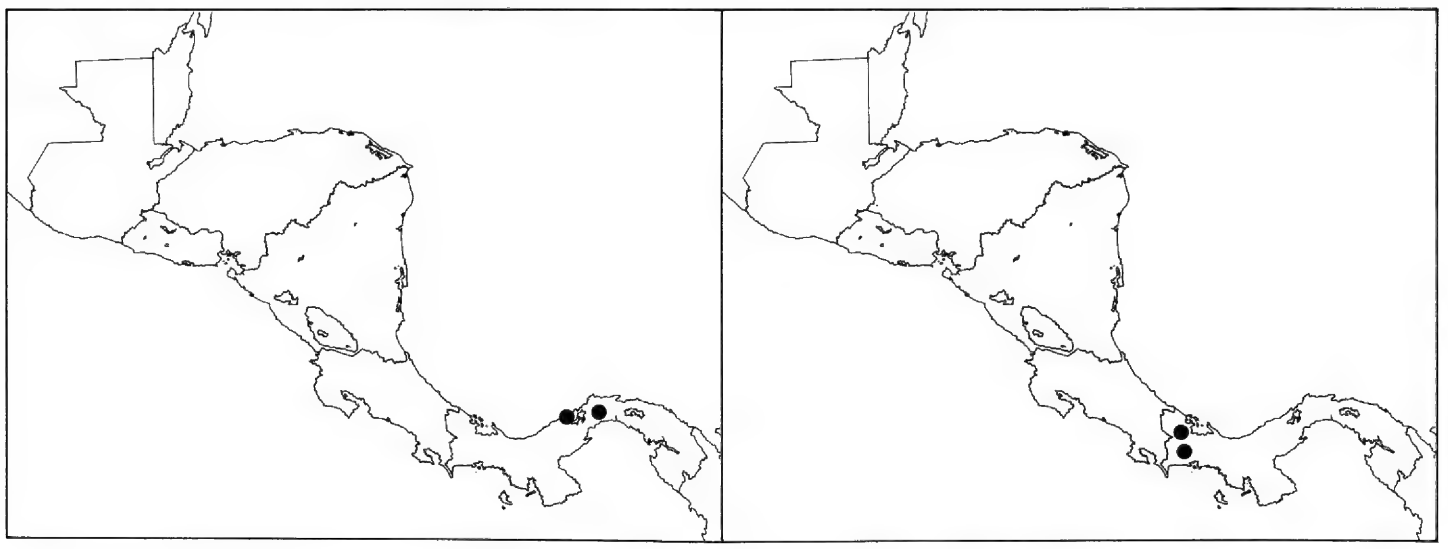


Figure 149. *Brymela complanata*. A. Habit. B, D & E. Leaves. C. Leaf apex. F. Median leaf cells. G. Basal and alar cells. H. Stem in cross section. Scale in mm: bar = 0.05 (C, F, G); bar = 0.08 (H); bar = 0.28 (B, D, E); bar = 1.56 (A). All figure parts from *Crosby 4475*.



Brymela complanata *Brymela crosbyi*

cells linear-flexuose, porose, to 60 µm long; basal cells near the insertions oblong-rectangular to long-rectangular; alar cells undifferentiated. Dioicous. Setae elongate, 1.5–2.0 cm long, red, smooth. Capsules inclined, symmetric and cylindric, neck well developed, 1.5–2.0 mm long; exothecial cells oblong to rounded-rectangular, incrassate, more or less collenchymatous; stomata rudimentary, 4–6-celled, on neck; operculum and annulus not seen; peristome diplolepideous; exostome teeth narrowly triangular with broad median furrows, densely and closely striate below, coarsely papillose above, ventral surface hyaline to yellowish, smooth to lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, cilia absent or rudimentary. Spores rounded, 12–18 µm, papillose. Calyptra not seen.

Illustration. Figure 149.
Habitat. On lianas and tree bases; 213–720 m.
Distribution in Central America. PANAMA. Colón: *Crosby 10316* (FH, MO, NY, PMA, US); Panamá: *Davidse & D'Arcy 10107B* (MO).
World range: Central America.

Brymela complanata is a small species, with strongly creeping primary stems, short, erect, sparsely branched secondary stems, and distinctly complanate leaves. There is no other Central American species of *Brymela* with this combination of features, which gives the plants an aspect more like *Mittenothamnium* or *Taxiphyllum*. However, the long double costae, smooth, porose leaf cells, absence of foliose pseudoparaphyllia, and strongly furrowed exostome teeth indicate *Brymela.* This species is most similar to the Caribbean *Brymela fissidentoides* (Hook. f. & Wilson) W. R. Buck. That species, though, has more closely spaced, considerably larger (1.8–2.7 mm vs. 0.9–1.2 mm), oblong-lanceolate leaves.

3. *Brymela crosbyi* (B. H. Allen) B. H. Allen, *comb. nov. Hookeriopsis crosbyi* B. H. Allen, Bryologist 90: 45. 1987. Protologue. Panama. Prov. Chiriquí, along Holcomb Trail to Cerro Horqueta, vicinity of Campo Uno, north of Boquete, elev. 6,500 ft., *Crosby 4075*. Type. Panama. Along Holcomb Trail to Cerro Horqueta. Vicinity of Campo Uno. North of Boquete. Elevation–6500 feet, 14 iv 1966, *M. R. Crosby 4075* (MO, holotype).

Plants small, in green to pale green, glossy mats, becoming yellow green to reddish with age. Stems yellow, becoming red with age, closely adnate to substrate, to 30 mm long; stems in cross section with 2–3 rows of small, firm-walled epidermal cells, cortical cells hyaline, thin-walled, central strand absent; pseudoparaphyllia absent; paraphyllia absent; axillary hairs 2-celled, basal cell quadrate, brown, upper cell elongate, clavate, hyaline. Branches identical to stems, but frequently ending in a terminal mass of gemmae. Leaves 1–2 mm long, concave, uniform, erect to erect-spreading, branch leaves with terminal gemmae stiffly erect-appressed, lanceolate to elongate-triangular, gradually

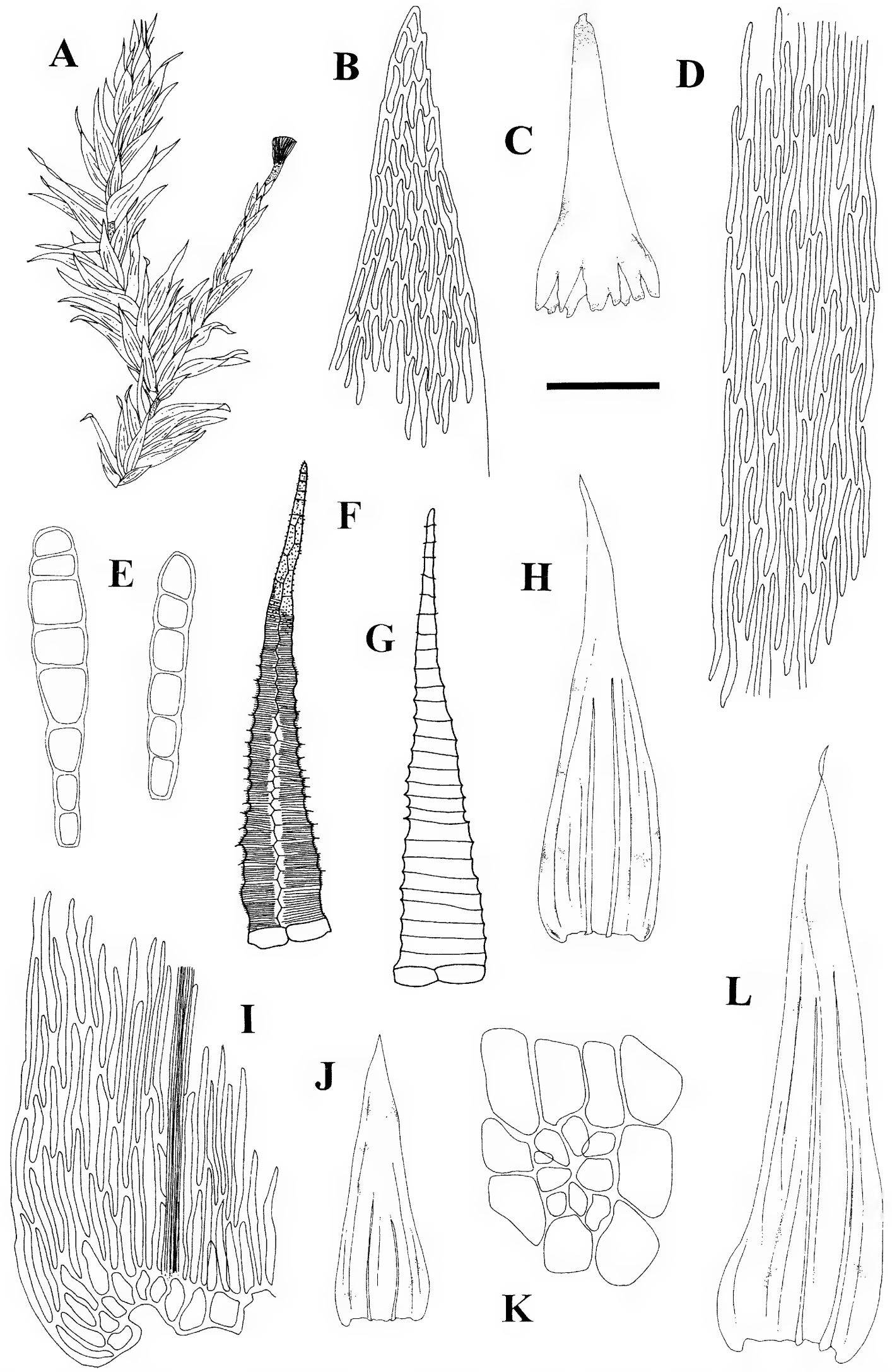


Figure 150. *Brymela crosbyi*. A. Habit. B. Leaf apex. C. Calyptra. D. Median leaf cells. E. Gemmae. F. Exostome, dorsal (outer) surface. G. Exostome, ventral (inner) surface. H & L. Leaves. I. Basal and alar cells, showing leaf plicae. J. Gemmiferous stalk leaf. K. Stoma. Scale in mm: bar = 0.05 (B, D, I, K); bar = 0.06 (E); bar = 0.09 (F, G); bar = 0.36 (C, H, J, L); bar = 1.56 (A). All figure parts from *Crosby 4075* (type).

long-acuminate, rounded to the insertion, strongly plicate when wet or dry; margins entire (occasionally weakly serrulate at apex), elimbate, plane; costae double, weak, to 2/3 the leaf length, one side often longer than the other, frequently difficult to distinguish from the leaf plicae; cells smooth, firm- to thick-walled, not or weakly porose, upper and median cells narrowly linear, 20–60 × 3–4 μm, basal margins shortly rectangular to more or less quadrate, usually with a band of orange red cells across the leaf insertions. Asexual reproduction by large, greenish to hyaline masses of gemmae at ends of branches; gemmae uniseriate, filiform, 5–14 cells long, cells rectangular to quadrate, firm-walled. Dioicous. Setae elongate, to 12 mm long, red, smooth. Capsules horizontal, oblong-cylindric, to 1.8 mm long, wrinkled at neck; exothecial cells broadly rectangular, collenchymatous; stomata 4–8-celled, on neck; opercula long-rostrate, to 1.8 mm long; annulus not seen; peristome diplolepideous; exostome teeth narrowly triangular, yellowish to red, with median furrows, densely and closely striate below, papillose above, median line present throughout, ventral surface yellowish hyaline, smooth, trabeculae well developed and projecting; endostome as long as the exostome, yellowish white, smooth below, lightly papillose above, basal membranes high, segments broad, keeled, weakly or not perforate, cilia absent. Spores rounded, 12–18 μm, faintly papillose. Calyptrae mitrate, yellowish white, lobed at base, naked, with a few short hairs at base, to 2 mm long.

Illustrations. Allen (1987d, Figs. 1–13). Figure 150.

Habitat. On rotting wood, decomposing trunks, and fallen trees; 800–1981 m.

Distribution in Central America. PANAMA. Bocas del Toro: *Allen 5851* (MO); Chiriquí: *Salazar et al. 5613* (MO).

World range: Central America.

Brymela crosbyi is a small species with erect, non-rugose leaves that are strongly plicate when wet or dry. Its leaves have entire (sometimes weakly serrulate) margins and faint costae (often obscured by the leaf plicae) that extend more or less two-thirds the leaf length. The costae are smooth at back, do not project at the tips, and often one fork is longer than the other. The most distinctive feature of the species is the presence of numerous gemmiferous branches with stiffly erect-appressed, weakly costate leaves and terminal clusters of uniseriate gemmae. It is the only species of *Brymela* with terminal clusters of gemmae, which otherwise occurs in Central American Hookeriaceae only in some species of *Crossomitrium*. That genus differs from *H. crosbyi* in having ecostate leaves and stems with a hyalodermis.

The leaves of *B. angustiretis*, *B. websteri*, and *B. crosbyi* are somewhat similar in shape, and all three species have faint costae that are smooth at back. *Brymela angustiretis* and *B. websteri* differ from *B. crosbyi* in having non-plicate leaves that are often rugose to undulate. Their leaves also differ from *B. crosbyi* in having denticulate to serrulate upper margins. The costae of *Brymela websteri* further differ from those of *B. crosbyi* by often weakly projecting at the apex.

4. *Brymela laevinervis* (Renauld & Cardot) B. H. Allen, *comb. nov. Hookeriopsis laevinervis* Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32(1): 196. 1893 [1894]. Protologue. [Costa Rica] Forêts du Rio Naranjo (*Pitt.*[*ier*] *n^o^ 5663*). Types. Forêt de Naranjo, 1893, *Tonduz* [*Pittier*, *Fl. Costaricensis*] *5663* [ex herb. Cardot] (FH, isotype); Forêts du Rio Naranjo, leg. *Tonduz*, 1893, *Fl. Costar. n. 5663* (NY, isotype).

Plants medium-sized, 2–4 cm long, green to yellowish green, occasionally yellowish red, in dense, glossy mats. Stems prostrate, irregularly branched, thick, hyaline to yellowish when young, becoming reddish with age; stems in cross section with epidermis of 2–3 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2 cells long, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect-incurved, twisted and rugose when dry, ovate- to oblong-lanceolate, acuminate, abruptly pinched at base of acumina, 1.5–2.0 mm long; margins serrate above, serrulate to subentire below, plane to erect, incurved at base of acumina, rounded at base; costae double, thin, ending 3/4 the leaf length, diverging throughout, smooth on back, not or weakly projecting at the tips; cells smooth, median cells long-rectangular to linear, at times flexuose,

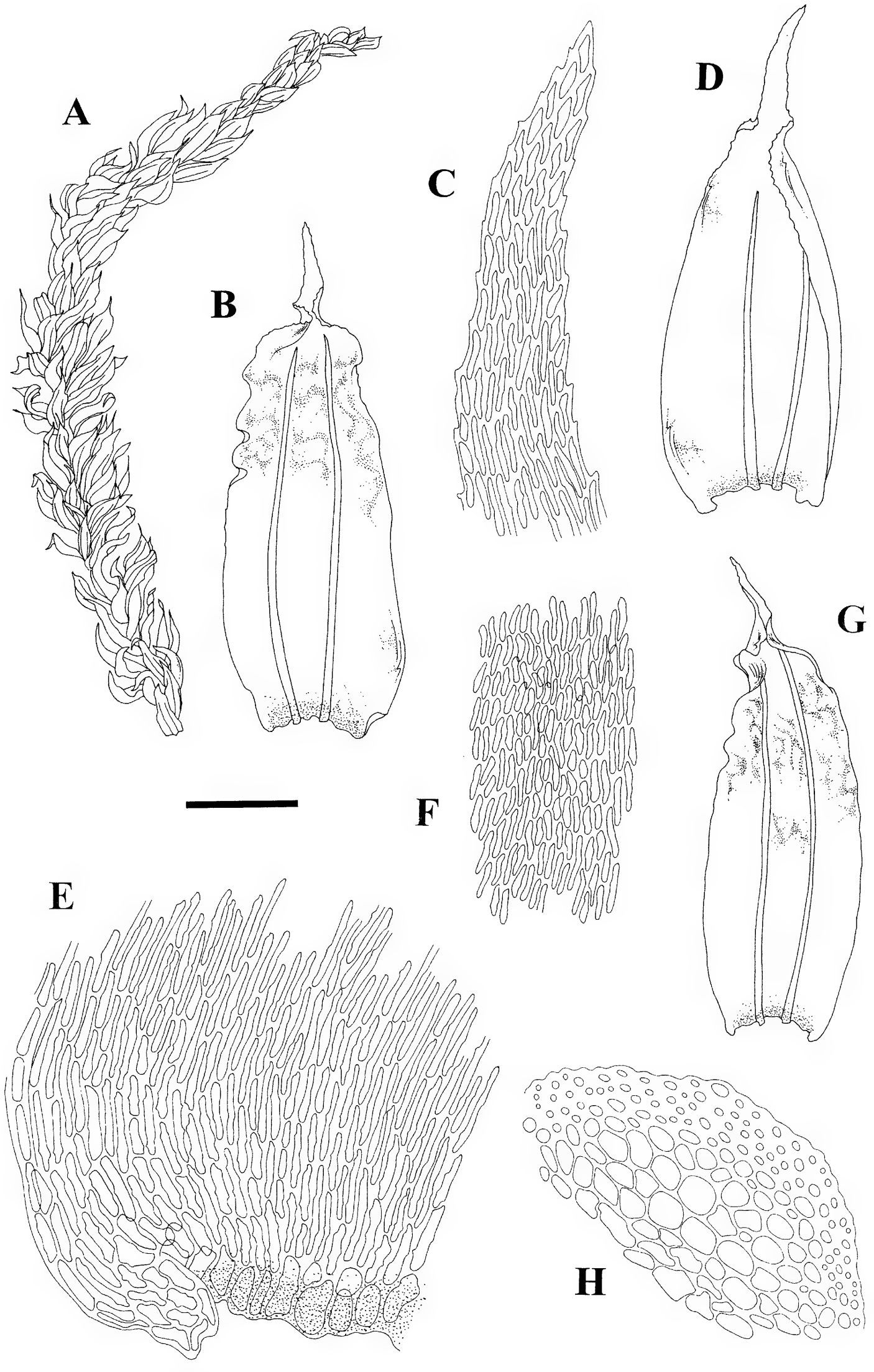
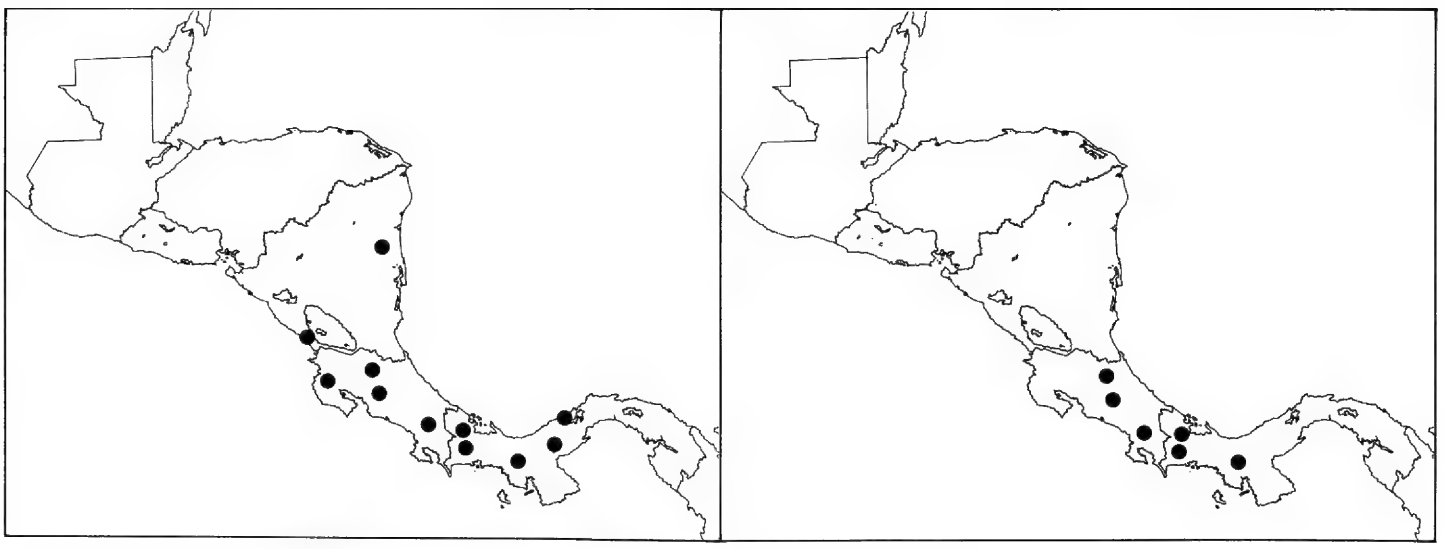


Figure 151. *Brymela laevinervis*. A. Habit. B, D & G. Leaves. C. Leaf apex. E. Basal and alar cells. F. Median leaf cells between costae. H. Stem in cross section. Scale in mm: bar = 0.06 (C, E, F); bar = 0.08 (H); bar = 0.4 (B, D, G); bar = 1.56 (A). F from *Tonduz 5663*; B, H from *Herrera 1017*; G from *Folsom 6455*; all other figure parts from *Allen 5095B*.



Brymela laevinervis *Brymela obtusifolia*

14–40 × 3–4 μm, firm-walled, sometimes porose; basal cells longer, cells near the insertions oblong-rectangular to long-rectangular; alar cells undifferentiated. Dioicous. Setae elongate, 2.0–2.5 cm long, red, smooth below, roughly papillose to tuberculate on capsule neck and upper part of setae. Capsules inclined, symmetric and cylindric, neck well developed, 2.0–2.5 mm long; exothecial cells oblong to rounded-rectangular, incrassate, more or less collenchymatous; rudimentary 2–4-celled stomata on neck; operculum and annulus not seen; peristome diplolepideous; exostome teeth narrowly triangular, with broad median furrows, densely and closely striate below, coarsely papillose above, ventral surface hyaline to yellowish, smooth to lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, cilia absent or rudimentary. Spores rounded, 16–20 μm, papillose. Calyptra not seen.

Illustration. Figure 151.

Habitat. On tree trunks and branches, logs, and rotting branches; 200–1600 m.

Distribution in Central America. NICARAGUA. Rivas: *Granzow de la Cerda GC-1658* (DUKE, MO); Zelaya: *Stevens 4893A* (MO). COSTA RICA. Alajuela: *Herrera 1017* (MO); Guanacaste: *Dauphin 2579* (MO); Puntarenas: *Crosby 2700* (CR, MO); San José: *Crosby & Crosby 5878* (CR, MO, NY). PANAMA. Bocas del Toro: *Allen 5095B* (MO); Chiriquí: *Allen 5453A* (MO); Coclé: *Folsom & Collins 6478* (MO, NY, PMA); Colón: *Crosby 10449* (MO); Veraguas: *Mori & Kallunki 3251* (MO).

World range: Central America.

Brymela laevinervis is a medium-sized species with irregularly, but sometimes densely branched stems. Its ovate- to oblong-lanceolate leaves are erect, incurved-twisted, and strongly rugose when dry. The leaves of *B. laevinervis* have serrate margins, and the apices are short- or long-acuminate. The most distinctive feature of the species is found at the base of leaf acumina, where the margins are distinctly and strongly pinched inward. The double costae are long and thin, divergent throughout, smooth at back, and usually projecting at the tips as short spines.

In Central America *B. laevinervis* differs from all other *Brymela* species in having leaves that are abruptly constricted at the base of the acumen. *Brymela angustiretis* and *B. websteri* are similar to *B. laevinervis* in having ovate-lanceolate, rugose leaves with thin costae that are smooth at back. The leaves of *B. angustiretis*, in addition to being gradually acuminate, are not nearly as rugose as those of *B. laevinervis* and have longer (30–70 μm vs. 14–40 μm) leaf cells. *Brymela websteri* differs from *B. laevinervis* in having narrower, falcate-secund leaves that are gradually long and narrowly acuminate. The costae in *B. websteri* also differ from those of *B. laevinervis* in usually more or less merging or ending very near the upper margins.

The South American *Brymela cuspidata* (A. Jaeger) W. R. Buck and *B. laevinervis* have similarly shaped leaves, and in both the leaves are abruptly constricted at the base of the acumina. Buck (1987)

synonymized the two species, but *B. cuspidata* differs from *B. laevinervis* in having costae that are crested or stoutly toothed on the upper dorsal surface.

5. *Brymela obtusifolia* (E. B. Bartram) W. R. Buck, Brittonia 39: 218. 1987. *Hookeriopsis obtusifolia* E. B. Bartram, Contr. U.S. Natl. Herb. 26: 101. 1928. Protologue. On wet rocks, Cerro de las Caricias, north of San Isidro, Province of Heredia, Costa Rica, *Paul C. Standley* and *Juvenal Valerio*, March 11, 1926, *no. 52068*. Types. On wet rocks, Cerro de las Caricias, north of San Isidro, Province of Heredia, March 11, 1926, *Paul C. Standley & Juvenal Valerio*, *No. 52068* (US, holotype; FH, NY, isotypes).

Plants small, 1–3 cm long, green, yellowish green, rarely yellowish red, in thin or dense glossy mats. Stems prostrate, irregularly branched, thick, hyaline to yellowish when young, becoming reddish with age; stems in cross section with epidermis of 2–3 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2–3 cells long, basal cell short-rectangular, reddish brown, upper cell(s) oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves falcate-secund, slightly plicate when dry, oblong-ovate, rounded to obtuse, 1.0–1.5 mm long; margins sinuate to subentire above, entire below, plane; costae double, stout, ending 2/3–3/4 the leaf length, diverging throughout, smooth on back, not projecting at the apices; cells smooth, upper cells linear-flexuose, 30–80 × 3–4 µm, firm-walled, cells between the costae similar to cells near the margins; basal cells near the insertions oblong-rectangular to long-rectangular; alar cells undifferentiated. Dioicous. Perigonia and perichaetia sessile along stems and branches. Setae elongate, 2–3 cm long, red, smooth below, papillose-roughened below the capsule. Capsules more or less inclined, symmetric and cylindric, neck well developed, 1.5 mm long; exothecial cells oblong to rounded-rectangular, incrassate, more or less collenchymatous; stomata 2–4-celled, on neck; opercula long-rostrate, conic at base, 0.7–1.5 mm long; annuli massive, persistent, of 4–6 rows of yellowish, hexagonal cells; peristome diplolepideous; exostome teeth narrowly triangular with broad median furrows, densely and closely striate below, coarsely papillose above, ventral surface hyaline to yellowish, smooth to lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, perforate, cilia absent or rudimentary. Spores rounded, 10–15 µm, smooth to faintly papillose. Calyptrae mitrate, irregularly lobed, reddish and lightly roughened above, yellowish below, 1.5–2.0 mm long.

Illustrations. Bartram (1928a, Fig. 32 F–L); Churchill and Linares (1995, Fig. 34 a–d). Figure 152.

Habitat. On rocks and boulders along or in streams and on rocks in forests; 620–1600 m.

Distribution in Central America. COSTA RICA. Cartago: *Crosby & Crosby 5817* (MO); Heredia: *Standley & Valerio 52068* (FH, NY, US); Puntarenas: *Lyon 549* (CR, MO). PANAMA. Bocas del Toro: *Allen 5117* (MO); Chiriquí: *McPherson 6825D* (MO); Veraguas: *Crosby 10202* (MO).

World range: Central America; Western and Northern South America.

Brymela obtusifolia is a small species that commonly occurs on rocks in and along streams. Its leaves are distinctly falcate-secund, which gives the plants an aspect similar to the Sematophyllaceae. The presence of long, thick, double costae, thick, mitrate calyptrae, and the absence of alar cell differentiation, as well as endostomial cilia, place the species in the Hookeriaceae. The stems of *Brymela obtusifolia* are remarkably thickened and whitish for a considerable distance below the apical buds, which gives them the appearance of having a stem hyalodermis. This aspect of the plants may be due to their rheophytic habitat. However, although the epidermal cells are somewhat enlarged, they are thick-walled. The leaf apices of *B. obtusifolia* vary from broadly obtuse to rounded-acute, and most collections have leaves that exhibit nearly the entire range of apical form. The hookeriaceous peristome of *B. obtusifolia* differs from the peristome of other members of *Brymela* in having broadly perforate endostomial segments. The presence of falcate-secund leaves that are obtuse to broadly acute distinguishes *B. obtusifolia* from all other Central American species of *Brymela.*

6. *Brymela tutezona* Crosby & B. H. Allen, Monogr. Syst. Bot. Missouri Bot. Gard. 11: 211. 1985.

Protologue. Panama. Veraguas: N of Santa Fé, summit of Cerro Arizona, 1570 m, *Hammel 4740.*

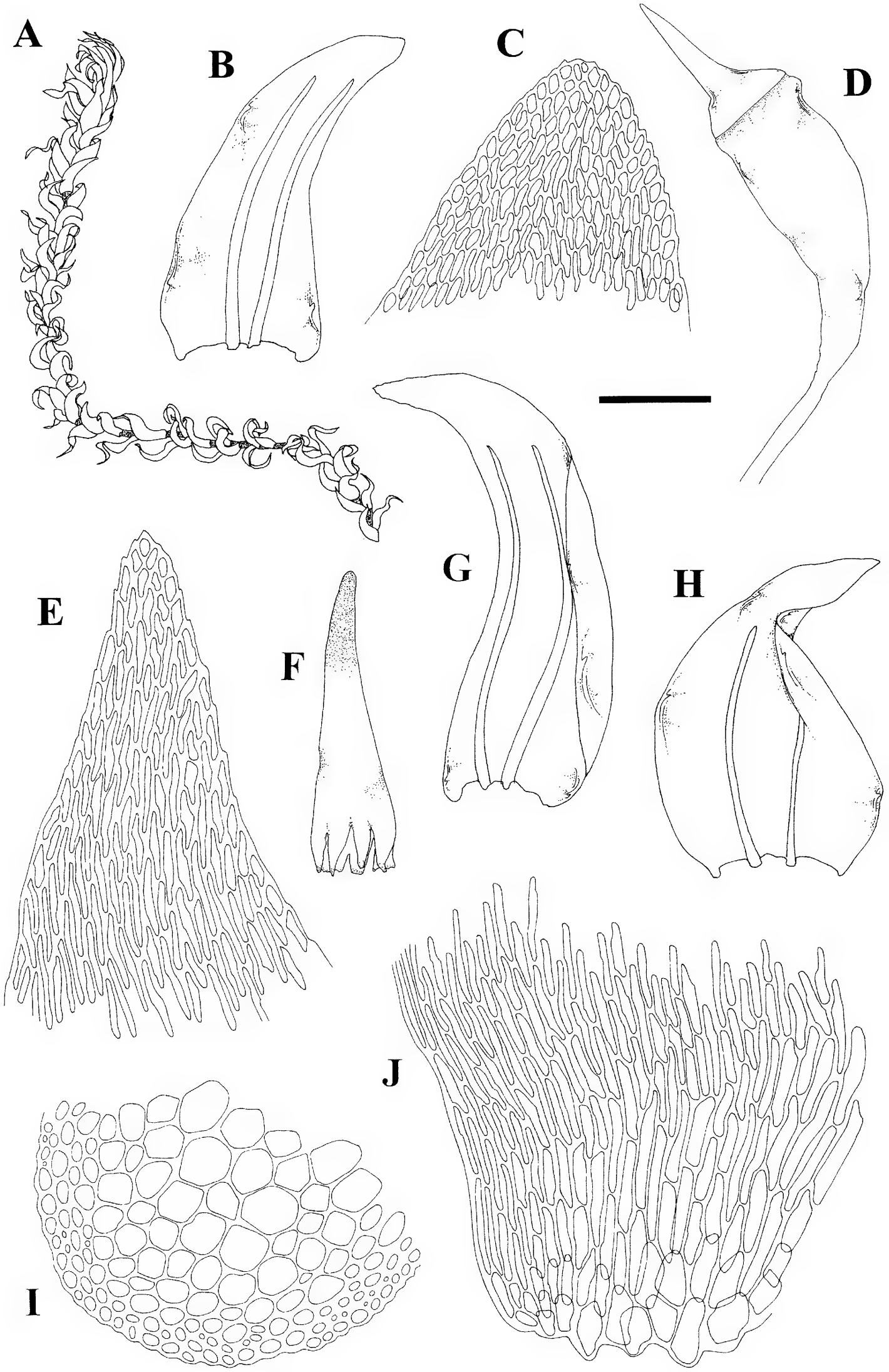


Figure 152. *Brymela obtusifolia*. A. Habit. B, G & H. Leaves. C & E. Leaf apices. D. Seta, capsule, and operculum. F. Operculum. I. Stem in cross section. J. Basal and alar cells. Scale in mm: bar = 0.06 (C, E, J); bar = 0.08 (I); bar = 0.6 (D, F); bar = 0.71 (B, G, H); bar = 1.56 (A). B from *Standley 52068*; H from *McPherson 6825D*; C, I from *Nee 14394*; all other figure parts from *Crosby 5817*.

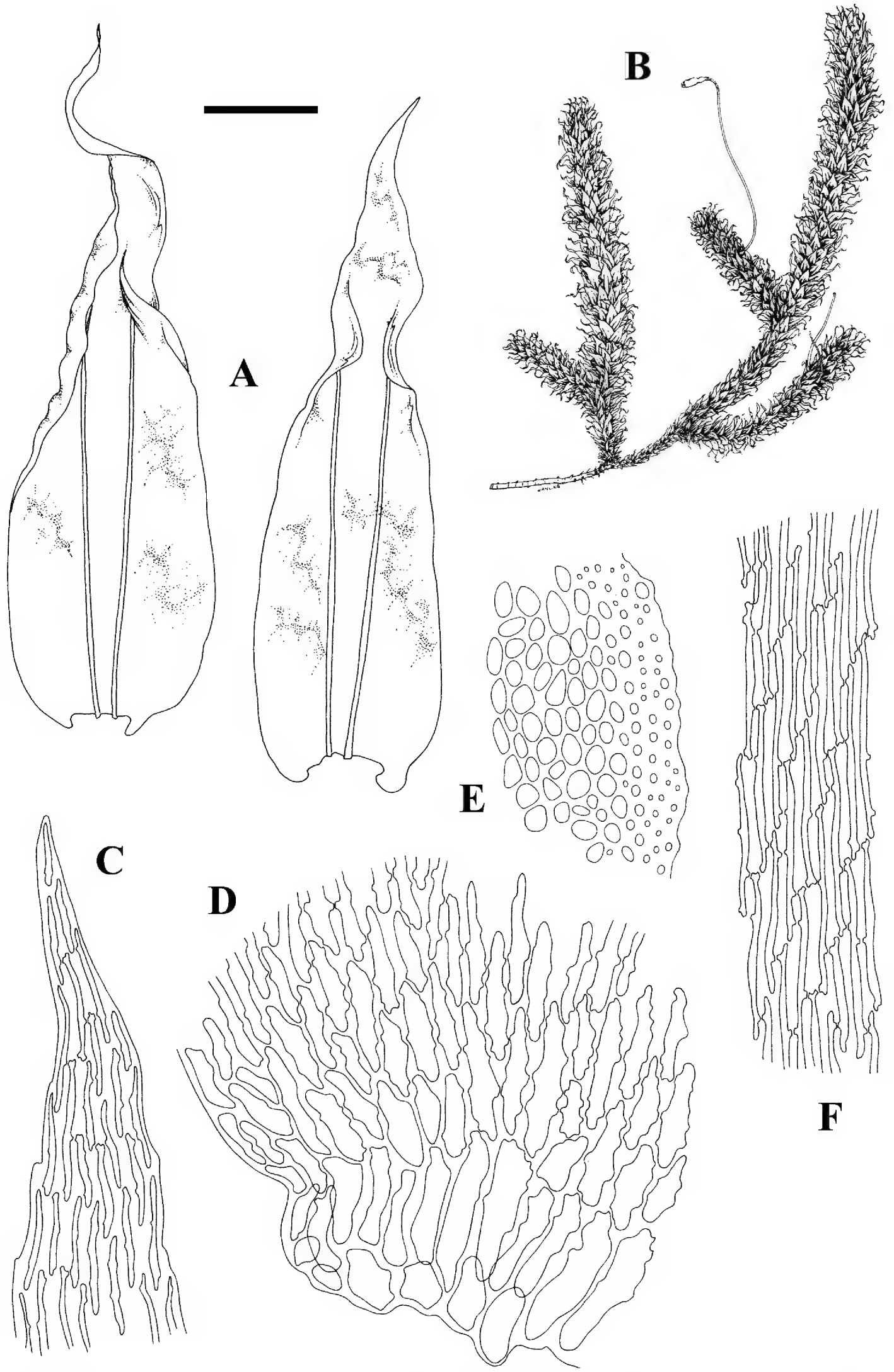
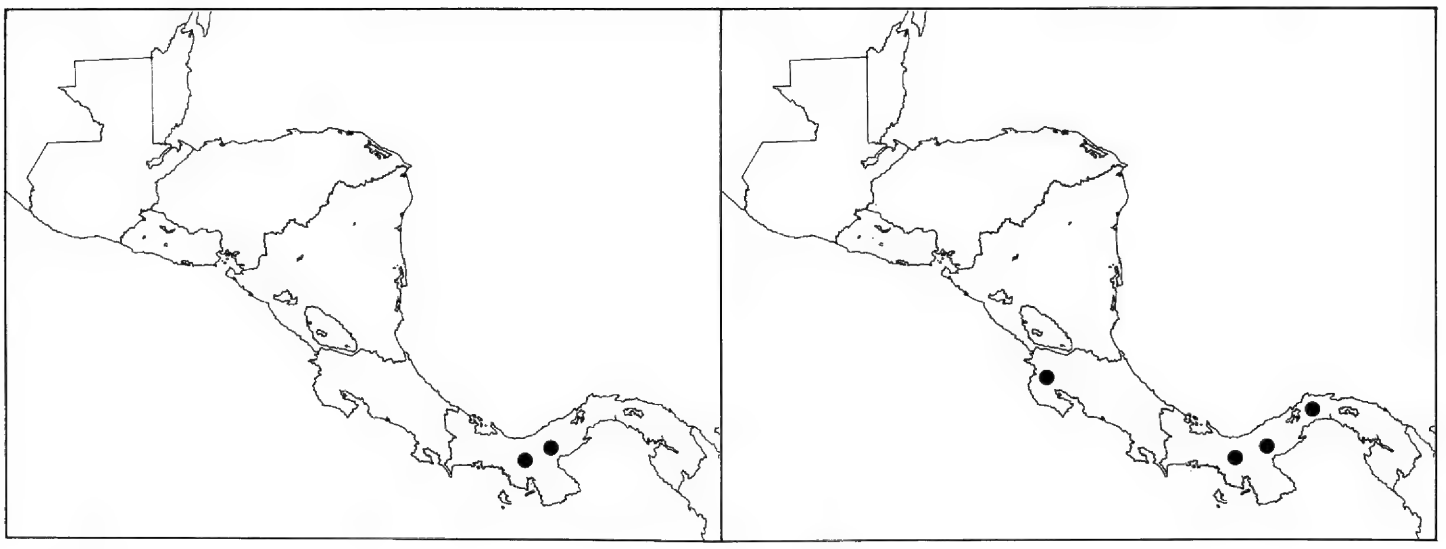


Figure 153. *Brymela tutezona*. A. Leaves. B. Habit. C. Leaf apex. D. Basal and alar cells. E. Stem in cross section. F. Median leaf cells. Scale in mm: bar = 0.06 (C, D, F); bar = 0.08 (E); bar = 1.0 (A); bar = 15 (B). A, E from *McPherson 12089C*; B from *Hammel 4740* (type); all other figure parts from *Hammel 8571*.



Brymela tutezona *Brymela websteri*

Types. Panama. Veraguas. N of Santa Fé, Summit of Cerro Arizona, heath-like terrain formed by the dense crowns of elfin forest trees packed with bromeliads, ferns, lycopodium, mosses (*Sphagnum*), elev. 4700 ft., 10 Sept. 1978, *B. Hammel 4740* (MO, holotype; BM, DUKE, NICH, PMA, isotypes).

Plants robust, to 11 cm long and 0.8–1.3 cm wide, yellow green above, red to burgundy below, in glossy epiphytic masses. Stems creeping, irregularly branched, hyaline to yellowish when young, becoming reddish with age, evenly foliate; stems in cross section with sclerodermis of 3–4 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2–4 cells long, basal 1–3 cells short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids in sparse groups from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect, strongly undulate above, plicate below when dry, erect-spreading when wet, symmetric or weakly asymmetric, concave, broadly ovate-lanceolate, long-acuminate, 6–8 × 2–3 mm; margins entire below, weakly serrate above, plane; costae double, thin, ending 1/2–3/4 the leaf length, diverging throughout, smooth on back, not projecting at the apices; cells smooth, incrassate, porose, apical cells rhomboidal to elongate-rhomboidal, 39–69 × 9–12 μm, median cells linear-rhomboidal, 55–115 × 7–9 μm, cells across the base reddish orange, rectangular, strongly porose; alar cells shortly rectangular, 23–55 × 13–21 μm. Dioicous. Perigonia sessile along stems and branches. Perichaetia terminal on lateral buds. Setae elongate, 2.5–3.0 cm long, dark red, scabrous above. Capsules more or less inclined, symmetric and cylindric, neck moderately developed, 2.5–3.5 mm long; exothecial cells rounded-rectangular, incrassate, more or less collenchymatous; stomata on neck; opercula long-rostrate, conic at base, 1.5–2.0 mm long; annuli massive, persistent, of 4–8 rows of yellowish, hexagonal cells; peristome diplolepideous; exostome teeth narrowly triangular, with broad median furrows, densely and closely striate below, coarsely papillose above, ventral surface hyaline to yellowish, smooth; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not perforate, cilia absent. Spores rounded, 23–35 μm, faintly papillose. Calyptra not seen.

Illustrations. Crosby and Allen (1985, Figs. 1–6). Figure 153.

Habitat. Epiphytic on leaves and branches of trees and shrubs; 890–1570 m.

Distribution in Central America. PANAMA. Coclé: *McPherson 11970* (MO); Veraguas: *McPherson 12089C* (MO, NY).

World range: Central America.

Brymela tutezona is a very robust species with stems reaching 11 cm long. Plants of *B. tutezona* have strongly creeping primary stems and erect, robust secondary stems that occasionally bear

branches. On stripping the leaves from most plants, however, numerous primordia are found at regular intervals along the secondary stems. Its plants usually have a remarkable reddish to burgundy color, are evenly foliate, and have long (6–8 mm), broadly ovate-lanceolate, strongly undulate leaves. The leaves are broadly rounded to the insertions (sometimes weakly auriculate) and have long leaf cells that are remarkably incrassate and porose throughout. The costae of *B. tutezona* are relatively weak, reaching 1/2–3/4 the leaf length, they are smooth at back, and they project at the tips. The leaf margins are mostly plane and serrulate above. *Brymela tutezona* has elongate, dark red setae that are scabrous above and inclined capsules. The opercula are long-rostrate and the massive annuli consist of 4–8 rows of yellowish, hexagonal cells.

There is no other Central American species of *Brymela* that approaches the size of *B. tutezona*. Indeed, the northern South American *B. parkiana* (Hook. & Grev.) W. R. Buck (known also from Barbados) is the only *Brymela* species that comes close to *B. tutezona* in size. Although *B. parkiana* sometimes has creeping stems to 10 cm long, the leaves are obtuse to acute rather than long-acuminate, and they are never more than 3 mm long.

Hemiragis aurea is similar to *Brymela tutezona* in size, and it has a non-complanate habit, incrassate, porose leaf cells, and leaves that are rounded at base. It differs from *B. tutezona* in having non-undulate, strongly plicate, long-triangular leaves that are only 3–5 mm long. Although some species of *Thamniopsis* also approach *B. tutezona* in size, that genus differs from *B. tutezona* in having a well-developed stem hyalodermis and thin-walled leaf cells that are greatly enlarged and bulging at base.

7. *Brymela websteri* (H. A. Crum & E. B. Bartram) W. R. Buck, Brittonia 39: 218. 1987. *Hookeriopsis websteri* H. A. Crum & E. B. Bartram, Bull. Inst. Jamaica, Sci. Ser. 8: 52. 1958. Protologue. Portland: Mist forest on rough limestone rocks 1000–1500 ft. alt., John Crow Mountains. 1.5 miles southwest of Ecclesdown, Jamaica. *Grady L. Webster 5199*, August 7, 1954. Types. Mist forest on rough limestone rocks, alt. 1000–1500 ft., John Crow Mts., 1.5 mi. SW of Ecclesdown, Portland Parish, August 6, 1954, *Grady L. Webster 5199* (FH, isotype); Portland Parish: John Crow Mountains, east slope, ca. 1.5 mi SW of Ecclesdown; mist forest on rough limestone rocks, alt. 1500 feet, 6 August 1954, *Grady L. Webster 5199* (NY, isotype).

Plants medium-sized, 2–5 cm long, yellow green, golden, or reddish yellow, in dense mats. Stems creeping, irregularly branched, hyaline to yellowish when young, becoming reddish with age, evenly foliate; stems in cross section with sclerodermis of 3–4 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2–3 cells long, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids in sparse groups from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves homomallous to falcate-secund, undulate, erect-spreading when dry or wet, symmetric, concave, lanceolate to ovate-lanceolate, long-acuminate, 2–3 mm long; margins serrulate above, subentire to entire below, plane, occasionally erect to slightly incurved above; costae double, slender, ending 2/3–3/4 the leaf length, diverging throughout, and usually ending on or very near the margins, smooth on back, weakly projecting at the apices; cells smooth, upper cells incrassate, porose, long-rectangular to sublinear, flexuose, 40–50 × 3–4 µm, cells across the base rectangular, strongly porose; alar cells shortly rectangular. Dioicous. Perigonia and perichaetia sessile along stems and branches. Setae elongate, 2–3 cm long, dark red, smooth. Capsules more or less inclined, symmetric and cylindric, neck moderately developed, 1.5–2.0 mm long; exothecial cells rounded-rectangular to rectangular, incrassate, more or less collenchymatous; stomata 2–4-celled, on neck; opercula long-rostrate, conic at base, 1.5 mm long; annuli massive, persistent, 4–6 rows of yellowish, hexagonal cells; peristome diplolepideous; exostome teeth narrowly triangular, with broad median furrows, densely and closely striate below, coarsely papillose above, ventral surface hyaline to yellowish, smooth; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not perforate, cilia absent. Spores rounded, 14–19 µm, faintly papillose. Calyptrae mitrate, irregularly lobed, reddish and lightly roughened, yellowish below, 2 mm long.

Illustrations. Crum and Bartram (1958, Figs. 21–22); Buck (1998, Pl. 20 9–16). Figure 154.

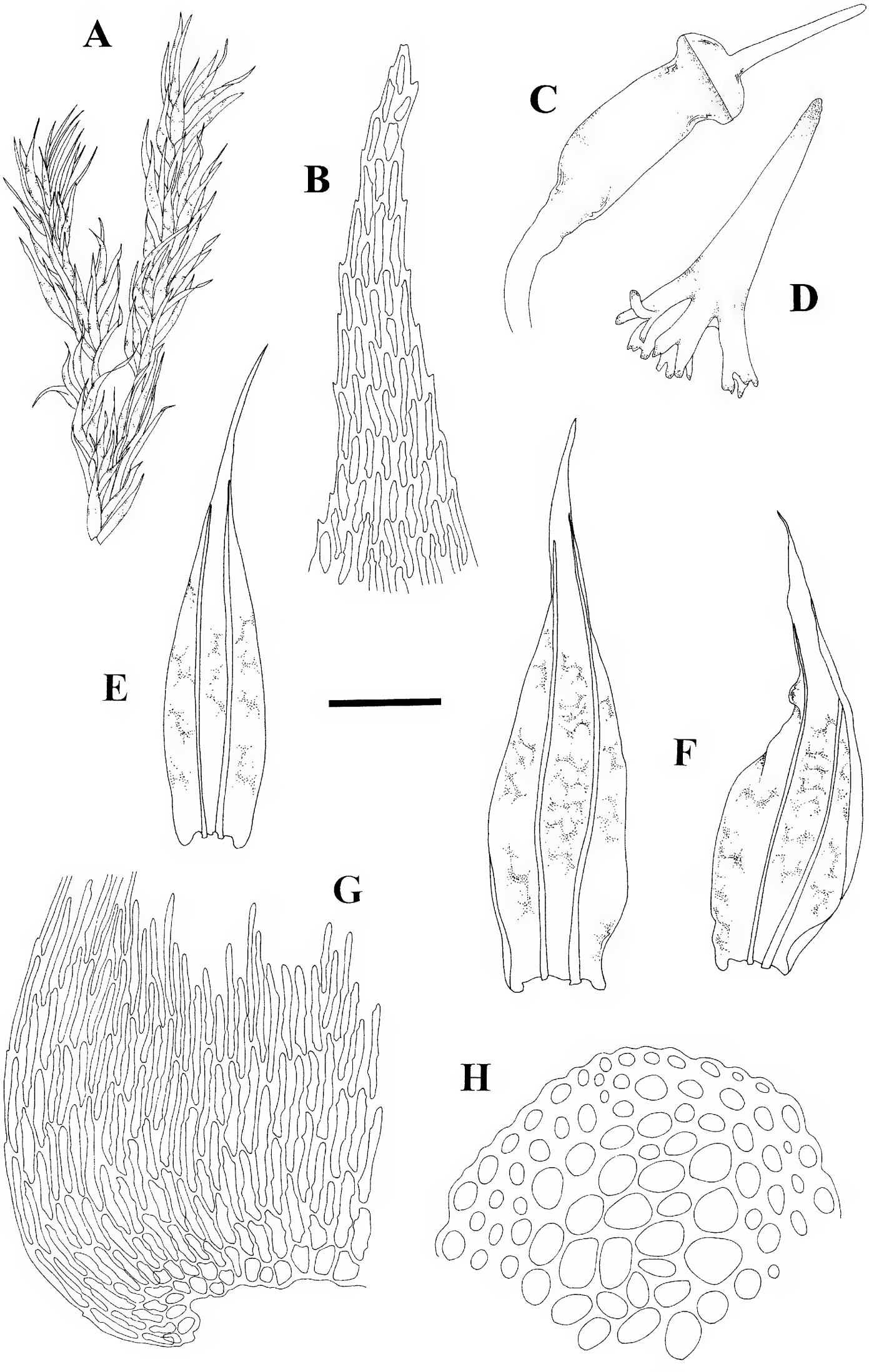


Figure 154. *Brymela websteri*. A. Habit. B. Leaf apex. C. Seta, capsule, and operculum. D. Calyptra. E & F. Leaves. G. Basal and alar cells. H. Stem in cross section. Scale in mm: bar = 0.06 (B, G, H); bar = 0.5 (E, F); bar = 0.9 (C, D); bar = 2.5 (A). C, D from *Rios 83*; F from *Allen 4943*; all other figure parts from *Allen 9028*.

Habitat. On trunks, branches, and twigs of trees and on rotting wood; 700–1000 m.

Distribution in Central America. COSTA RICA. Guanacaste: *Rios 83* (MO). PANAMA. Coclé: *Croat 67564* (MO, PMA); Panamá: *Allen 9028* (MO, PMA); Veraguas: *Nee 11271* (MO).

World range: Central America; Caribbean.

Brymela websteri is a small to medium-sized species with strongly creeping primary stems and erect, irregularly spaced secondary stems. Its plants often have a golden reddish color and evenly foliate, lanceolate to ovate-lanceolate, distinctly undulate leaves. Although the leaves are typically falcate to falcate-secund, they also can be erect-spreading, and sometimes both types of leaves are found in single collections. Distinctive leaf features of *B. websteri* include its slenderly long-acuminate apices and linear-flexuose, incrassate, and porose cells. The thin costae diverge throughout the leaf, are smooth at back, end on or near the upper margins, and often slightly project at the tips. The leaf margins are mostly plane and serrulate above. *Brymela websteri* has elongate, dark red, smooth setae and inclined capsules. The opercula are long-rostrate, and the massive annuli consist of 4–6 rows of yellowish, hexagonal cells.

In Central America *Brymela laevinervis* and *B. angustiretis* can be mistaken for *B. websteri*, because they all have ovate-lanceolate, rugose leaves with thin costae that are smooth at back and do not or faintly project at the tips. *Brymela laevinervis* differs from *B. websteri* in having leaves that are abruptly constricted at the base of the acumen and shorter leaf cells (14–30 µm vs. 40–50 µm). *Brymela angustiretis* differs from *B. websteri* in having broader, erect-spreading leaves that are broadly acuminate. The costae in *B. angustiretis* are also shorter than those of *B. websteri*; they end well away from the leaf margins, and they never project at the tips.

4. *Callicostella* (Müll. Hal.) Mitt., J. Proc. Linn. Soc., Bot. Suppl. 1: 136. 1859, conserved name. *Hookeria* Sm. sect. *Callicostella* Müll. Hal., Syn. Musc. Frond. 2: 216. 1851. *Hookeria* Sm. subgen. *Callicostella* (Müll. Hal.) Hampe, Verh. Zool.-Bot. Ges. Wien 21: 392. 1871.

Schizomitrium Schimp. *in* B.S.G., Bryol. Eur. 5: 59. 1851 (fasc. 46–47).

Plants small to medium-sized, green, yellowish green, reddish yellow, or red, in loose or dense, dull or glossy mats. Stems prostrate, often complanate-foliate, subpinnately or irregularly branched, hyaline to yellowish when young, becoming red with age; stems in cross section with sclerodermis of 2–5 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia foliose or subfoliose; axillary hairs 2–3 cells long, basal 1–2 cells short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves usually strongly dimorphic, with lateral leaves differing considerably from dorsal and ventral leaves, erect, erect-spreading, incurved-contorted, flexuose, smooth or undulate, asymmetric or symmetric, ovate, oblong to oblong-ovate, or ovate-lingulate, occasionally lingulate or obovate, obtusely rounded, occasionally truncate, broadly or narrowly acute, at times apiculate or pinched below apex, sometimes short-acuminate; margins serrulate, serrate, or irregularly erose-serrate in upper 2/3, subentire to entire below, plane, narrowly recurved above, or broadly incurved on one side at base, rounded at base; costae double, strong, ending 3/4–7/8 the leaf length, diverging throughout, parallel, or converging at the tips, smooth, serrate, or sharply toothed to serrate-crested on back, often projecting at the tips; upper cells stoutly unipapillose, lightly prorate or smooth, isodiametric, subhexagonal, oval-hexagonal, oblong-hexagonal, long-hexagonal, or oblong-elongate, firm-walled; basal cells short- to long-rectangular, or elongate, smooth or porose; alar cells undifferentiated. Autoicous, synoicous, or dioicous. Setae elongate, red or orange, smooth or scabrous throughout, at times smooth below and roughened above near capsule. Capsules inclined, symmetric and broadly cylindric, neck well developed; exothecial cells quadrate, oblong, or rounded-rectangular, incrassate, collenchymatous; stomata rudimentary, 3–6-celled, on neck; opercula conic-rostrate; annuli massive, of numerous rows of thin-walled, quadrate cells, persistent at the base of the opercula; peristome diplolepideous; exostome teeth narrowly triangular, with broad median furrows, densely and closely striate below, coarsely papillose above, dorsal surface red, ventral surface hyaline to yellowish, smooth to lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, seg-

ments broad, strongly keeled, not or weakly perforate, cilia absent. Calyptrae mitrate, irregularly lobed, laciniate, or fimbriate-laciniate at base, often scabrous roughened above, naked or sparsely hairy.

Callicostella is a genus of 97 species (Crosby *et al.* 2000); it occurs throughout the tropical and subtropical regions of the world. Approximately two-thirds of these species are known from the Neotropics, but the genus has been greatly over-described and there may be as few as fifteen species of *Callicostella* in that area. *Callicostella* typically is found mixed with other mosses on rotting logs or growing terrestrially. The species exhibit incredible variation both within and between collections, which probably accounts for the over-description of the genus. Plants of *Callicostella* are usually small in size, loosely complanate, and they can be dark green, green, yellowish green, or reddish in color. Its stems have a sclerodermis and foliose to subfoliose pseudoparaphyllia. A distinctive feature of *Callicostella* is the high degree of leaf di- or trimorphism found in most species. The lateral leaves are typically the largest and, for the most part, they best demonstrate the distinctive features of the species. The dorsal and ventral leaves are often radically different from the lateral leaves in shape, areolation, costal form, and marginal form. They are, in fact, often so different from the lateral leaves that it is difficult to imagine they came from the same plant; only the lateral leaves should be used when evaluating species. The lateral leaves in *Callicostella* are seldom more than 1.5 mm long; they can be symmetric or asymmetric, undulate or flat, and are often incurved-contorted when dry. They vary in shape from ovate, oblong, ovate-lingulate, or lingulate to obovate, with obtuse-rounded, acute, or broadly acuminate apices. The leaf margins vary from serrulate to serrate or erose-serrate, and often the teeth are swollen and bifid. The leaves are elimbate and have long costae that usually end near the apex. The costae are sometimes divergent, parallel, or strongly convergent at the tips; they can be smooth, serrate, or serrate-crested at back, and often project at the tips. The leaves of *Callicostella* typically have a more or less homogeneous areolation, in which the upper and median cells are short, often isodiametric, firm- or thick-walled and the basal cells are gradually enlarged. The cells can be distinctively unipapillose, weakly prorate, or smooth. Most Central American species of *Callicostella* have smooth or weakly prorate leaf cells (*C. callicostelloides*, *C. merkelii*, *C. rufescens*), but papillose leaf cells are often associated with the genus, because the most common species (*C. pallida* and *C. oerstediana*) have papillose leaf cells. *Callicostella* has elongate setae that can be smooth or scabrous throughout, or smooth below and papillose-roughened near the capsule. The capsules of *Callicostella* are distinctive in having a massive annulus that is persistent on the operculum and consists of numerous rows of yellowish, quadrate cells. As in other members of the Hookeriaceae, the rudimentary stomata are made up of 3–6 cells. *Callicostella* has a typical hookeriaceous peristome. The calyptrae are mitrate, irregularly lobed to laciniate-fringed at base, and sometimes sparsely hairy.

In Central America *Callicostella* can be confused with *Thamniopsis*, *Brymela*, or *Trachyxiphium.* All three genera differ from most species of *Callicostella* in having smooth leaf cells and usually weaker costae. *Thamniopsis* and *Callicostella* also have a massive annulus in which the annular cells are persistent on the opercula. *Thamniopsis* further differs from *Callicostella* in having a hyalodermis rather than a sclerodermis on the outside layer of the stems. *Brymela* differs from most species of *Callicostella* in having elongate, often porose leaf cells and weakly toothed leaf margins with teeth that are never swollen or bifid. Typically, *Brymela* has smooth costae that only weakly project at the tips. *Trachyxiphium* differs from *Callicostella* in having elongate cells that are often prorate. Allen and Crosby (1986a) considered *Callicostella* extremely close to *Pilotrichidium.* Indeed, the two genera are remarkably similar in plant size, leaf form, leaf areolation, and costal form. All species of *Pilotrichidium*, however, differ from *Callicostella* in having a stem hyalodermis and entire leaf margins. In addition, the most common Central American species, *Pilotrichidium callicostatum*, has pluripapillose leaf cells.

The name *Callicostella* combines the generic name *Callicosta* with the Latin substantival suffix *-ella* (indicating diminutive).

1. Leaf cells smooth throughout, or smooth below and weakly prorate above 2
1. Median and/or upper leaf cells papillose, papillae centered over the lumina 5

2. Leaves often undulate; margins irregularly erose-serrate in upper 2/3 . . . . . 2. *C. callicostelloides*
2. Leaves flat or crispate; margins regularly serrulate above 3

3. Leaves lanceolate to ovate-lanceolate; apices abruptly acute to short-acuminate . . . . . 1. *C. bernoullii*
3. Leaves ovate, oblong, or obovate; apices truncate, rounded, or obtuse 4

4. Upper leaf cells oblong to short-fusiform, median leaf cells between costae oblong to oblong-elongate; costae divergent throughout, or weakly convergent at the tips . . . . . 6. *C. rufescens*
4. Upper leaf cells oval-hexagonal to oblong-hexagonal, median leaf cells between costae hexagonal to rhombic; costae strongly converging at tips. . . . . 3. *C. merkelii*

5. Leaf margins irregularly erose-serrate in upper 2/3 of leaf. . . . . 4. *C. oerstediana*
5. Leaf margins regularly serrulate above. . . . . 5. *C. pallida*

1. *Callicostella bernoullii* (Hampe) Broth., Nat. Pflanzenfam. I(3): 937. 1907. *Hookeria bernoullii* Hampe *in* Müll. Hal., Bull. Herb. Boissier 5: 207. 1897. *Schizomitrium bernoullii* (Hampe) F. D. Bowers, Phytologia 56: 492. 1985. Protologue. [Guatemala] Mazatenango, Coll. [*Bernoulli*] *N*^{o} *70*. Types. Herbarium Guatemalense, *No. 70 Hookeria* (*Callicostella*) *Bernoullii* Schpr., Mazatenango, 1866–78 Coll. *Bernoulli & Cario* (NY *ex* GOET, isotype); *Hookeria Bernoullii* Müll. Hal., Guatemala. *Bernoulli* (NY, isotype); *Hookeria Bernoullii* Schimper, Chilion, Guatemala, *Bernoulli* 1867 (NY, 2 isotypes).

Hookeria bernoullii Schimp. *ex* A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1877–1878: 470. 1879, invalid name, lacks a description. *Cyclodictyon bernoullii* (Schimp. *ex* A. Jaeger) Kuntze, Rev. Gen. Pl. 2: 835. 1891, invalid combination.

Plants small, 1.0–2.0 cm long, green or yellowish green, in loose, glossy mats. Stems prostrate, irregularly branched, red with age; stems in cross section with epidermis of 2–3 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia subfoliose; axillary hairs 2 cells long, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves flexuose to inwardly subcrispate when dry, weakly dimorphic. Lateral and dorsal leaves wide-spreading, symmetric or weakly asymmetric, lanceolate to ovate-lanceolate, 1.0–1.4 mm long, apices abruptly acute to short-acuminate; margins serrate in upper 2/3, teeth somewhat swollen, serrulate to subentire below, plane throughout or plane above and narrowly recurved above on one side, rounded at base; costae double, strong, ending 3/4–7/8 the leaf length, diverging throughout, smooth or serrate on back, stoutly projecting at the tips; upper cells mostly weakly prorate, at times smooth, irregularly shaped, hexagonal, oblong, or irregularly short-rectangular, 14–30 × 4–10 µm, firm-walled, becoming larger toward the base, extreme basal cells short- to long-rectangular, 26–50 µm long, smooth; alar cells undifferentiated. Ventral leaves lanceolate, acuminate, symmetric; margins irregularly dentate by swollen teeth in upper 2/3, plane; costae double, slender, smooth at back, weakly projecting at the tips; upper cells lightly prorate to smooth, irregularly short-rectangular, thin-walled, becoming long-rectangular toward the base; alar cells undifferentiated. Autoicous or synoicous. Setae elongate, 7–14 mm long, orange when young, dark red with age, smooth throughout. Capsules inclined to horizontal, more or less symmetric, cylindric, neck well developed, 1.0 mm long; exothecial cells rounded-quadrate to oblong, incrassate, collenchymatous; stomata rudimentary, 3–5-celled, on neck; opercula conic-rostrate, 0.7 mm long; annuli massive, of 10–15 rows of thin-walled cells, separating from capsule along dehiscent zone at base, persistent on the operculum; peristome diplolepideous; exostome teeth narrowly triangular, with broad median furrows, densely and closely striate below, coarsely papillose above, dorsal surface dark red, ventral surface yellowish, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose, basal membranes high, segments broad, strongly keeled, not or weakly perforate, cilia absent. Spores rounded, 8–10 µm, smooth or lightly papillose. Calyptrae mitrate, slenderly lobed at base, smooth, naked, 2.0 mm long.

Illustrations. Welch (1966, Figs. 293–305); not Bartram (1949, Fig. 135 A–D = *Thamniopsis guatemalensis*); not Sharp *et al.* (1994, Fig. 591 f–i). Figure 155.

Habitat. On rotting bark.

Distribution in Central America. GUATEMALA. Suchitepéquez: *Bernoulli* (NY).

World range: Central America.

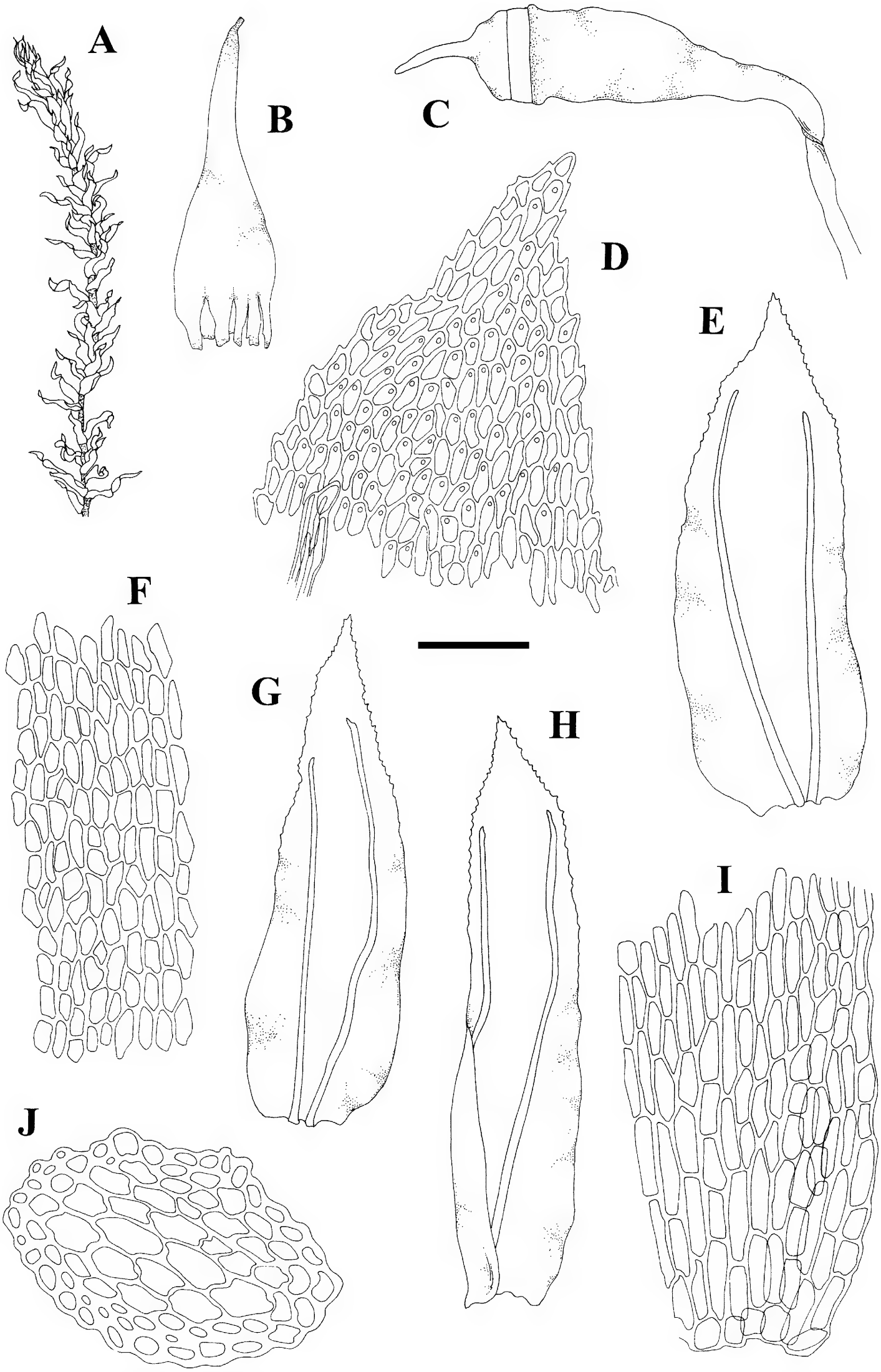
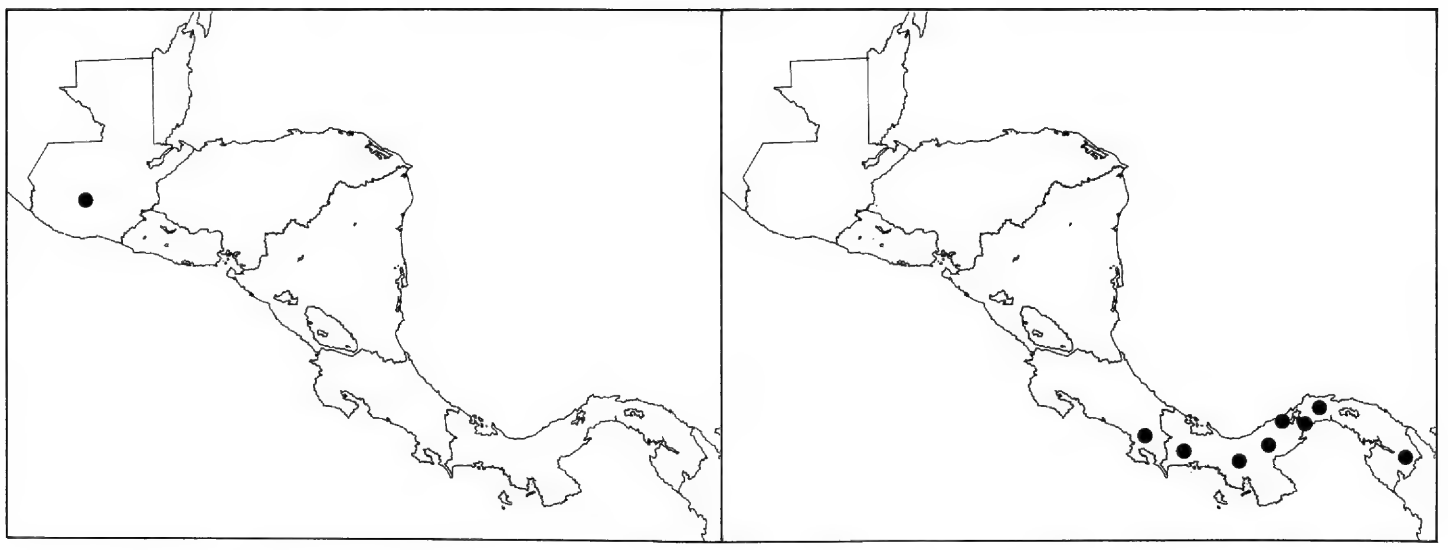


Figure 155. *Callicostella bernoullii*. A. Habit. B. Calyptra. C. Upper part of the seta, capsule, annulus, and operculum. D. Leaf apex. E, G & H. Leaves. F. Median leaf cells between the costae. I. Basal and alar cells. J. Stem in cross section. Scale in mm: bar = 0.06 (D, F, I, J); bar = 0.28 (E, G, H); bar = 0.5 (C); bar = 0.6 (B); bar = 1.56 (A). All figure parts from *Bernoulli 70* (type).



Callicostella bernoullii *Callicostella callicostelloides*

Callicostella bernoullii is known in Central America only from the type collection, which grew on rotting wood. It is a slender species, with stems that have a small sclerodermis and leaves that are flexuose to inwardly subcrispate when dry. The most distinctive feature of *C. bernoullii* is the presence of leaves with abruptly acute to shortly acuminate apices. However, leaf apical form in *Callicostella* is so variable that this distinction cannot be consistently used to recognize species without the benefit of additional distinguishing features. Other important features of *C. bernoullii* include its mostly lanceolate to ovate-lanceolate lateral leaves and fairly large, irregularly shaped, hexagonal, oblong, or irregularly short-rectangular, weakly prorate, upper leaf cells. The leaf margins are irregularly serrate, with somewhat swollen teeth. Sporophytically, *C. bernoullii* has elongate setae that are smooth throughout. The capsules in *C. bernoullii* have strongly collenchymatous exothecial cells and a massive annulus identical in form to that found in *Thamniopsis* and *Lepidopilum*.

In Central America the combination of narrow lateral leaves, with short-acuminate apices, and fairly large, weakly prorate upper leaf cells distinguishes *C. bernoullii* from the other regional species of *Callicostella*. There has been considerable confusion surrounding *Callicostella bernoullii*, *e.g.*, Bartram (1949) considered it to have smooth leaf cells, but all Guatemalan collections he cited as *C. bernoullii* are actually *Thamniopsis guatemalensis*. This species differs from *C. bernoullii* in having smooth leaf cells and a stem hyalodermis. Welch (1966) illustrated the type with single papillae over the lumina, but the types in NY have prorate leaf cells. *Callicostella bernoullii* has been reported from Oaxaca, Mexico (Bowers 1994). The illustrations of that species in Sharp *et al.* (1994) show plants with broadly acute leaves, papillae over the cell lumina, and shorter leaf cells than the types of *C. bernoullii*.

2. *Callicostella callicostelloides* (Herzog & Thér.) B. H. Allen, *comb. nov. Hookeriopsis callicostelloides* Herzog & Thér., Hedwigia 74: 110. 1934. *Brymela callicostelloides* (Herzog & Thér.) W. R. Buck, Brittonia 39: 217. 1987. Protologue. Panama: Cerro Canajague, Halbinsel Azuero, ca. 950 m [*C. Troll*]. Types. Panama, in peninsula Azuero, Cerro Canajague, ad arborum ramos, 950 m, IV. 1929, leg. *C. Troll* [Verdoorn, *Musci Selecti et Critici 25*] (FH, MO, NY, US, isotypes); Cerro Canajague, 900 m, Bergwald der Kasseerone, Halbinsel Azuero, leg. *C. Troll*, VI. 1929 (FH, isotype).

Hookeriopsis panamensis E. B. Bartram *in* B. Willis, Bryologist 42: 156. 1939. Protologue. [Panama] Barro Colorado Island, Canal Zone, January–February 1938, *Barbara Willis.* Types. Panama. On fallen tree, along brook parallel to Standley trail, Barro Colorado Island, 29 Jan. 1939 [sic], *Barbara Willis 42* (FH, holotype). Barro Colorado Island, Canal Zone, Jan.–Feb., 1938, *Barbara Willis* (FH, NY, US, isotypes).

Hookeriopsis welchiana H. A. Crum, Bryologist 89: 25. 1986. Protologue. Mexico. Puebla: Cerro de Cuhuatepec (southeastern Puebla), on decaying log, 3500 ft. alt., 23 Nov. 1964, *A. J. Sharp 1367aa.*

Plants medium-sized, 3–6 cm long, green to yellowish green, in dense dull mats. Stems prostrate, irregularly branched, thick, hyaline to yellowish when young, becoming red with age; stems in cross

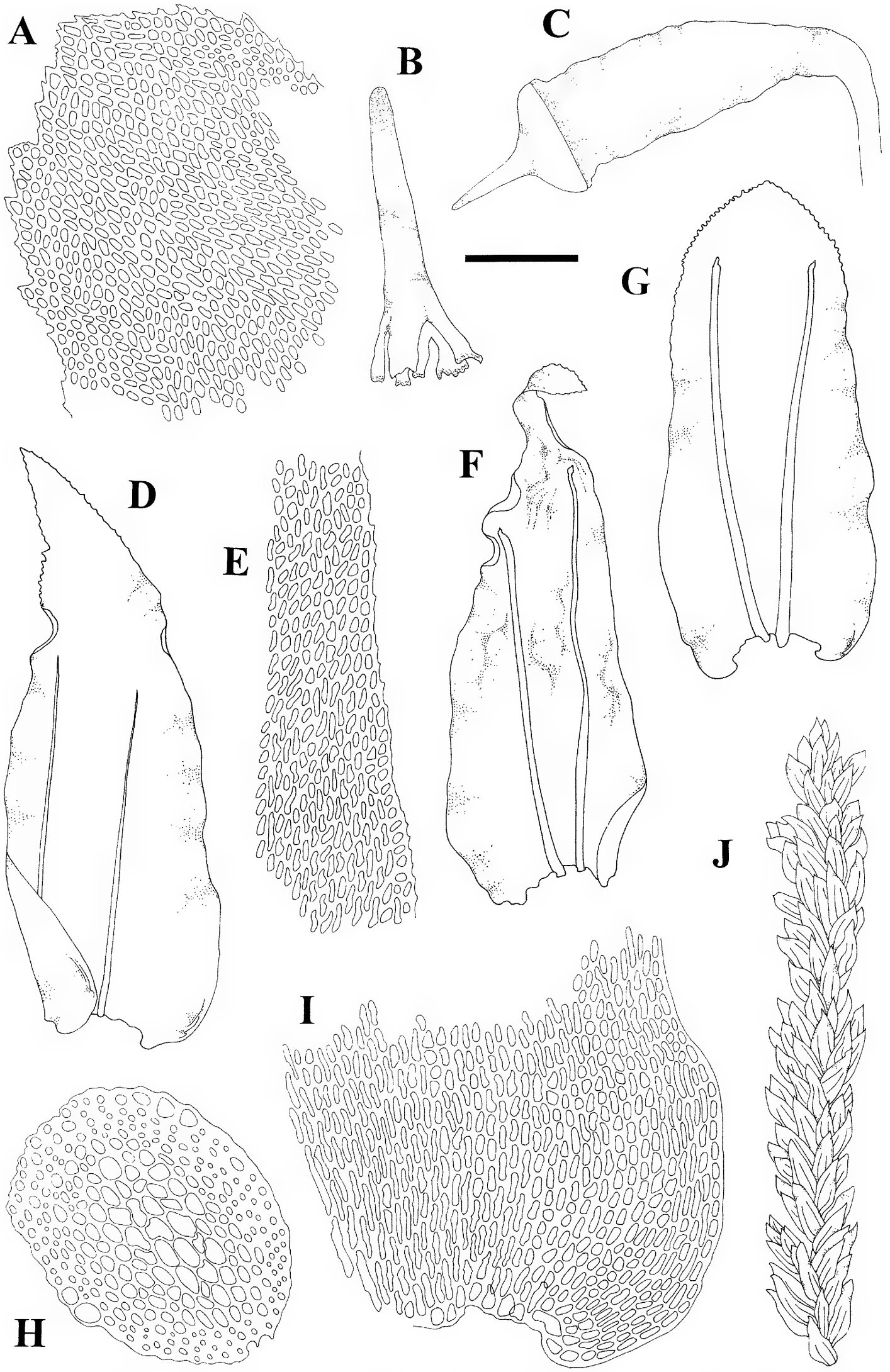


Figure 156. *Callicostella callicostelloides*. A. Leaf apex. B. Calyptra. C. Seta, capsule, and operculum. D, F & G. Leaves from same branch. E. Median leaf cells and margin. H. Stem in cross section. I. Basal and alar cells. J. Habit. Scale in mm: bar = 0.06 (A, E, I); bar = 0.08 (H); bar = 0.28 (D, F, G); bar = 0.6 (B, C); bar 1.56 (J). B from *Mori & Kallunki 2047*; C from *Hammel 4296*; all other figure parts from *Crosby 4347*.

section with epidermis of 3–5 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia foliose; axillary hairs 2–3 cells long, basal 1–2 cells short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect, somewhat curved-contorted, smooth or undulate when dry, oblong to ovate-oblong, occasionally lingulate, 1.2–1.8 mm long, obtusely rounded, broadly or narrowly acute, at times pinched below apices; margins irregularly erose-serrate in upper 2/3, subentire to entire below, plane or narrowly recurved above, rounded at base; costae double, strong, ending 3/4 the leaf length, diverging throughout, serrate on back, projecting at the tips; upper cells smooth or lightly prorate, irregularly shaped, isodiametric, subhexagonal, or oblong-hexagonal, 6–10 µm long, firm-walled; basal cells short- to long-rectangular, or elongate, smooth or porose; alar cells undifferentiated. Dioicous. Setae elongate, 15–25 mm long, red, smooth throughout. Capsules inclined, symmetric and broadly cylindric, neck well developed, 1–2 mm long; exothecial cells quadrate, oblong, or rounded-rectangular, incrassate, collenchymatous; stomata rudimentary, 3–6-celled, on neck; opercula conic-rostrate, 1.0 mm long; annuli well developed, of 3–4 rows of thin-walled, quadrate cells, persistent at the base of the opercula; peristome diplolepideous; exostome teeth narrowly triangular, with broad median furrows, densely and closely striate below, coarsely papillose above, dorsal surface red, ventral surface hyaline to yellowish, smooth to lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not or weakly perforate, cilia absent. Spores rounded, 10–16 µm, lightly papillose. Calyptrae mitrate, irregularly lobed at base, naked, 1.0 mm long.

Illustrations. Willis (1939, Fig. 5); Crum (1986, Figs. 12 & 13); Sharp *et al.* (1994, Fig. 599). Figure 156.

Habitat. On wet rocks along streams, rotting logs, tree buttress roots, and lianas; 50–800 m.

Distribution in Central America. COSTA RICA. Puntarenas: *Gentry & Burger 2797* (MO). PANAMA. Canal Area: *Lewis & Sharp 12* (MO, NY, PMA, US); Chiriquí: *Cornman 3008* (F, MO, US); Coclé: *Hunter & Allen* (FH); Colón: *Crosby 4473* (MO); Darién: *Gentry M-4* (MO, PMA); Panamá: *Crosby 4342* (FH, MO, NY, PMA, US); Veraguas: *Hammel 4296* (MO).

World range: Mexico; Central America.

Callicostella callicostelloides is a medium-sized species, with stems that have a very thick sclerodermis and foliose pseudoparaphyllia. Its leaves are erect to somewhat curved-contorted when dry; they can be flat to strongly undulate, and single collections can have some branches with flat leaves while others have undulate leaves. Leaf form is extremely variable in *C. callicostelloides*. Typically, the leaves are oblong to ovate-oblong, but occasionally they can be lingulate, with apices that vary from obtusely rounded to narrowly acute. Often the entire range in leaf form can be found in single collections or even single branches. The leaves have thick, double costae that are usually serrate at back and project at the tips. The upper leaf cells are firm-walled and remarkably variable in shape, but they are small (6–10 µm), more or less isodiametric, and often obscurely prorate near the apex. The basal leaf cells vary from short-rectangular with straight walls to elongate-flexuose with strongly porose walls.

Buck (1987) placed this species in *Brymela*, and the occasional elongate, porose basal leaf cells in *C. callicostelloides* support this placement. Furthermore, *Brymela rugulosa* (Mitt.) W. R. Buck closely resembles *C. callicostelloides* in overall aspect, and its leaves have erose dentate margins as well as costae that are serrate on back and project at the tips. *Brymela rugulosa* differs from *C. callicostelloides* in having long-rectangular upper leaf cells, often swollen marginal teeth, and leaf cells that are prorate in the upper two-thirds of the leaf. The genera have identical sporophytes; indeed, the generic placement of these species is not clear. The Central American species is here placed in *Callicostella* on the basis on its small, dense upper leaf cells and the presence of foliose pseudoparaphyllia.

Callicostella callicostelloides differs from all other Central American species of *Callicostella* in having the following combination of characters: presence of at least some acute leaves; irregularly erose-serrate upper leaf margins; small, dense upper leaf cells; leaf cells that are smooth or obscurely prorate near apex; and often porose basal leaf cells.

3. *Callicostella merkelii* (Hornsch.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 351. 1877. *Hookeria merkelii* Hornsch. *in* Mart., Fl. Bras. 1(2): 62. 1840. *Schizomitrium merkelii* (Hornsch.) J. Florsch., Fl. Suriname 6(1): 322. 1986. Protologue. [Brazil] In uliginosis ad terram prope Sebastianopolin, Julio et Augusto, c.fr. maturis: *Merkel.*

Callicostella vatteri E. B. Bartram, Bryologist 49: 118. 1946. *Schizomitrium vatteri* (E. B. Bartram) H. A. Crum, Bryologist 87: 208. 1984. Protologue. Guatemala. Dept. Zacapa: trail between Río Hondo and waterfall, alt. 250–400 m, *Steyermark 29473*. Types. Plants of Guatemala. Sierra de las Minas. Dept. Zacapa: trail between Río Hondo and waterfall, alt. 250–400 m, *Steyermark 29473* (FH, holotype; F, FH, isotypes).

Callicostella hondurensis H. A. Crum, Bryologist 55: 283. 1952. *Schizomitrium hondurense* (H. A. Crum) H. A. Crum, Bryologist 87: 209. 1984. Protologue. Honduras. Vicinity of El Zamorano, dept. Morazán, *Paul J. Shank*. Types. Central Honduras vicinity of El Zamorano, Morazan, *Paul J. Shank* (UBC, holotype; FH, NY, isotypes), *syn. nov.*

Callicostella mexicana H. Rob. & W. H. Welch, Bryologist 69: 9. 1966. Protologue. Mexico. Veracruz: Along the Tecolutla–Poza Rica road, 11.2 mi. E of Papantlla, *Pursell & Reese 5108*. Types. Jungly ravine and gorge, heavily wooded and strewn with limestone boulders, 11.2 mi. e. of Papantla along the Tecolutla–Poza Rica road, *Ronald A. Pursell 5108* (MO, US, isotypes), *syn. nov.*

Plants small to medium-sized, 1.0–3.0 cm long, green, yellowish green to green, in dense or loose mats. Stems prostrate, complanate-foliate, irregularly branched, thick, dark red; stems in cross section with epidermis of 2–3 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia subfoliose; axillary hairs 2 cells long, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves flexuose to inwardly contorted when dry, erect-spreading to spreading when wet. Lateral leaves asymmetric or symmetric, oblong to oblong-ovate, 1.0–1.5 mm long, obtusely rounded or acute, at times apiculate; margins serrulate above, subentire to entire below, plane above, broadly incurved on one side below, rounded at base; costae double, strong, ending 7/8 the leaf length, often converging at the tips and with tips usually parallel to the apical margins, smooth at back, usually projecting at the tips; cells smooth or weakly prorate near apex, firm-walled, upper cells irregularly shaped, oval-hexagonal to oblong-hexagonal, 10–20 µm long, median cells oval-oblong; basal cells enlarged, at times weakly bulging, subrectangular to rectangular, 15–35 µm long; alar cells undifferentiated. Dorsal and ventral leaves broadly ovate-lanceolate, 0.8–1.2 mm long, broadly acute. Autoicous or synoicous. Setae elongate, 1–2 cm long, orange to dark red, smooth below, roughened above near capsule. Capsules inclined, symmetric, oblong-cylindric, neck well developed, 1.0–1.5 mm long; exothecial cells rounded-quadrate to oblong, incrassate, collenchymatous; stomata rudimentary, 3–5-celled, on neck; opercula conic-rostrate, 1.0–1.2 mm long; annuli massive, of 15–20 rows of thin-walled cells, separating from capsule along dehiscent zone at base, persistent on the operculum; peristome diplolepideous; exostome teeth narrowly triangular, with broad median furrows, densely and closely striate below, coarsely papillose above, dorsal surface dark red, ventral surface hyaline to yellowish, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose, basal membranes high, segments broad, strongly keeled, not or weakly perforate, cilia absent. Spores rounded, 8–14 µm, smooth or lightly papillose. Calyptrae mitrate, laciniate at base, scabrous roughened above, naked, 1.5–2.0 mm long.

Illustrations. Hornschuch (1840, Pl. 3 I); Bartram (1949, Fig. 135 E–I); Crum (1952, Figs. 6–8); Welch (1966, Figs. 306–316); Florschütz-de Waard (1986, Fig. 125); Churchill (1994, Fig. 8 B); Sharp *et al.* (1994, Fig. 592); Vaz and Costa (2006a, Figs. 29–34). Figure 157.

Habitat. On tree trunks, rotting wood, soil, stream banks, and rocks in and along streams; 10–850 m.

Distribution in Central America. BELIZE. Cayo: *Dwyer & Liesner 12130A* (BRH, MO); Toledo: *Whittemore 6516* (BRH, MO, NY). EL SALVADOR. San Salvador: *Winkler 1* (MO). HONDURAS. Francisco Morazán: *Standley 21346* (F, MO). NICARAGUA. Zelaya: *Larue* (NY). COSTA RICA. Limón: *Crosby 3667A* (MO); San José: *Crosby 11413* (MO). PANAMA. Panamá: *Nee 6862* (MO).

World range: Mexico; Central America; Western and Northern South America, Brazil.

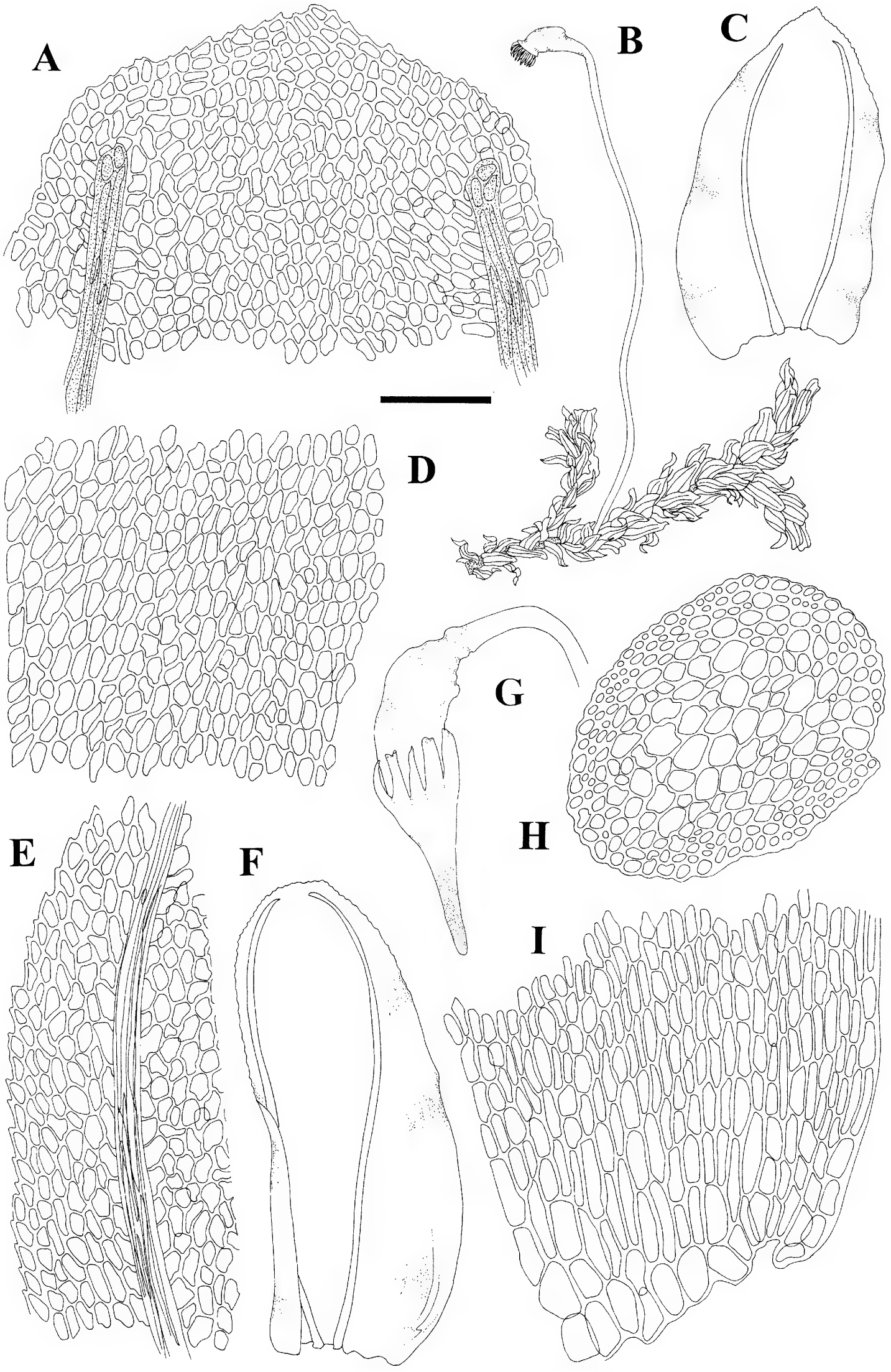
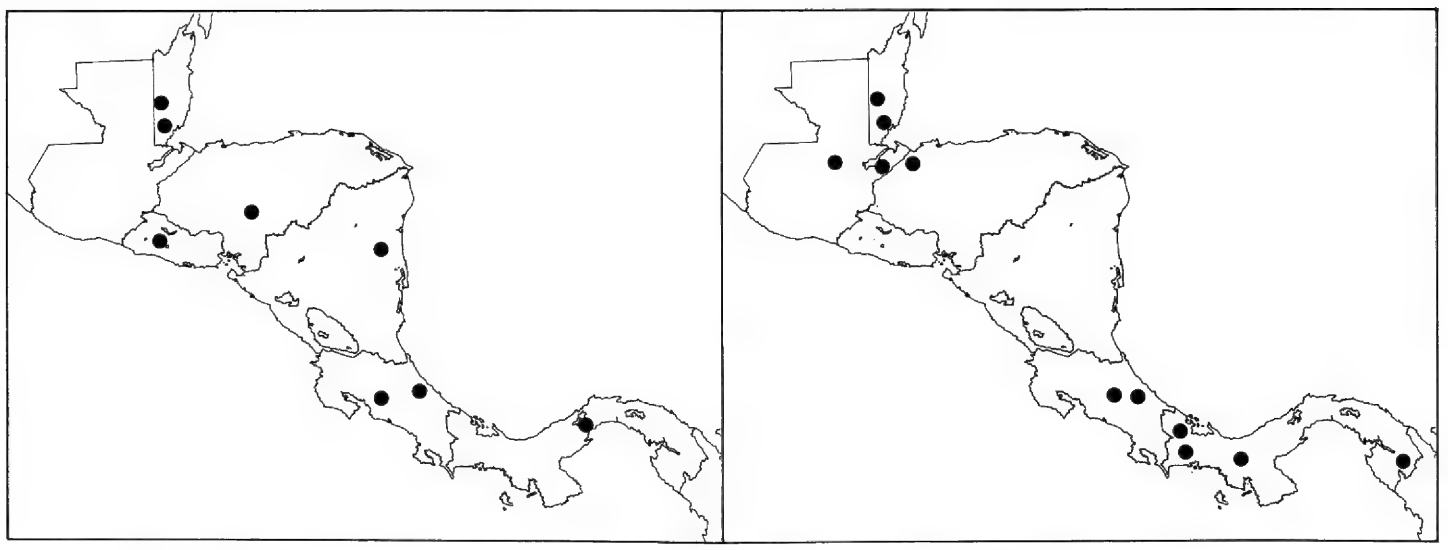


Figure 157. *Callicostella merkelii*. A. Leaf apex. B. Habit. C. Ventral leaf. D. Median leaf cells between costae. E. Upper leaf cells and margin. F. Lateral leaf. G. Seta, capsule, and calyptra. H. Stem in cross section. I. Basal and alar cells. Scale in mm: bar = 0.06 (A, D, E, I); bar = 0.09 (H); bar = 0.36 (C, F); bar = 0.9 (G); bar = 1.96 (B). B from *Allen 18865A*; D, E, I from *Steyermark 29473* (type *C. vatteri*); all other figure parts from *Crosby 3667A*.



Callicostella merkelii *Callicostella oerstediana*

Callicostella merkelii is widely distributed in Central America, but it is known from only a few localities. It grows on rotting logs as well as rocks in and along streams. The species has complanate-foliate stems, with oblong to oblong-ovate, obtusely rounded to broadly acute, often asymmetric lateral leaves. Its margins are plane above, with the basal margin usually broadly incurved below, and they are evenly serrulate above. Although its broadly obtuse leaves are distinctive, the costae in *C. merkelii* are perhaps its most distinctive feature. The costae are stout, end near the apex, and typically are so strongly converging above that the tips are parallel to the apical leaf margins. The costae are smooth at back and usually project at the tips. The upper leaf cells of *C. merkelii* are short and vary from oval-hexagonal to oblong-hexagonal. They are smooth throughout, or sometimes weakly prorate above. The setae in *C. merkelii* are smooth throughout or smooth below and roughed above near the capsule.

Crum (1952) gave the lateral leaf size of *Callicostella hondurensis* as 2.9–3.1 mm long, but the types of that taxon have lateral leaves no longer than 1.5 mm. The types of *C. vatteri* and *C. hondurensis* are identical. The plants in the type of *Callicostella mexicana* are considerably smaller than those in the types of *C. vatteri* and *C. hondurensis*. In addition, its leaves have weaker costae, more strongly serrulate upper margins, and they are often apiculate. Collections of *C. mexicana*, however, intergrade with typical forms of *C. merkelii*.

In Central America *C. merkelii* can be confused with the *aquatica*-form of *C. pallida*. The confusion of this form of *C. pallida* with *C. merkelii* is due to its broadly obtuse leaves that have evenly serrate upper margins. The form, however, has weakly papillose upper leaf cells that differ from those of *C. merkelii* in having the papillae centered over the lumina rather than prorate. In addition, the form has weaker costae that are usually divergent or parallel throughout or are convergent only at the extreme tips. *Pilotrichidium* is similar to *C. merkelii* in plant size, leaf form, leaf areolation, and costal form. All species of *Pilotrichidium*, however, differ from *Callicostella* in having entire leaf margins. In addition, the most common Central American species, *Pilotrichidium callicostatum*, has pluripapillose leaf cells.

4. *Callicostella oerstediana* (Müll. Hal.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 354. 1877. *Hookeria oerstediana* Müll. Hal., Syn. Musc. Frond. 2: 679. 1851. *Schizomitrium oerstedianum* (Müll. Hal.) H. A. Crum, Bryologist 87: 208. 1984. Protologue. Costa Rica Americae centralis, in reg. montosa inter 5000–8000′ ped. elevationis, mens. Febr. 1848. leg. *A. S. Oersted*. Type. Plantae Oersted. 1845–48. Costa Rica: Central America, in mts. between 5000–8000 ft. Feb. 1848, Coll. *A. S. Oersted* (NY, isotype).

Hookeria ciliata Schimp. *ex* Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 231. 1872. *Callicostella ciliata* (Schimp. *ex* Besch.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 353. 1877. *Schizomitrium ciliatum* (Schimp. *ex* Besch.) F. D. Bowers, Phytologia 56: 492. 1985. Protologue. [Mexico] Mirador (*Liebmann* in herb. Schimper).

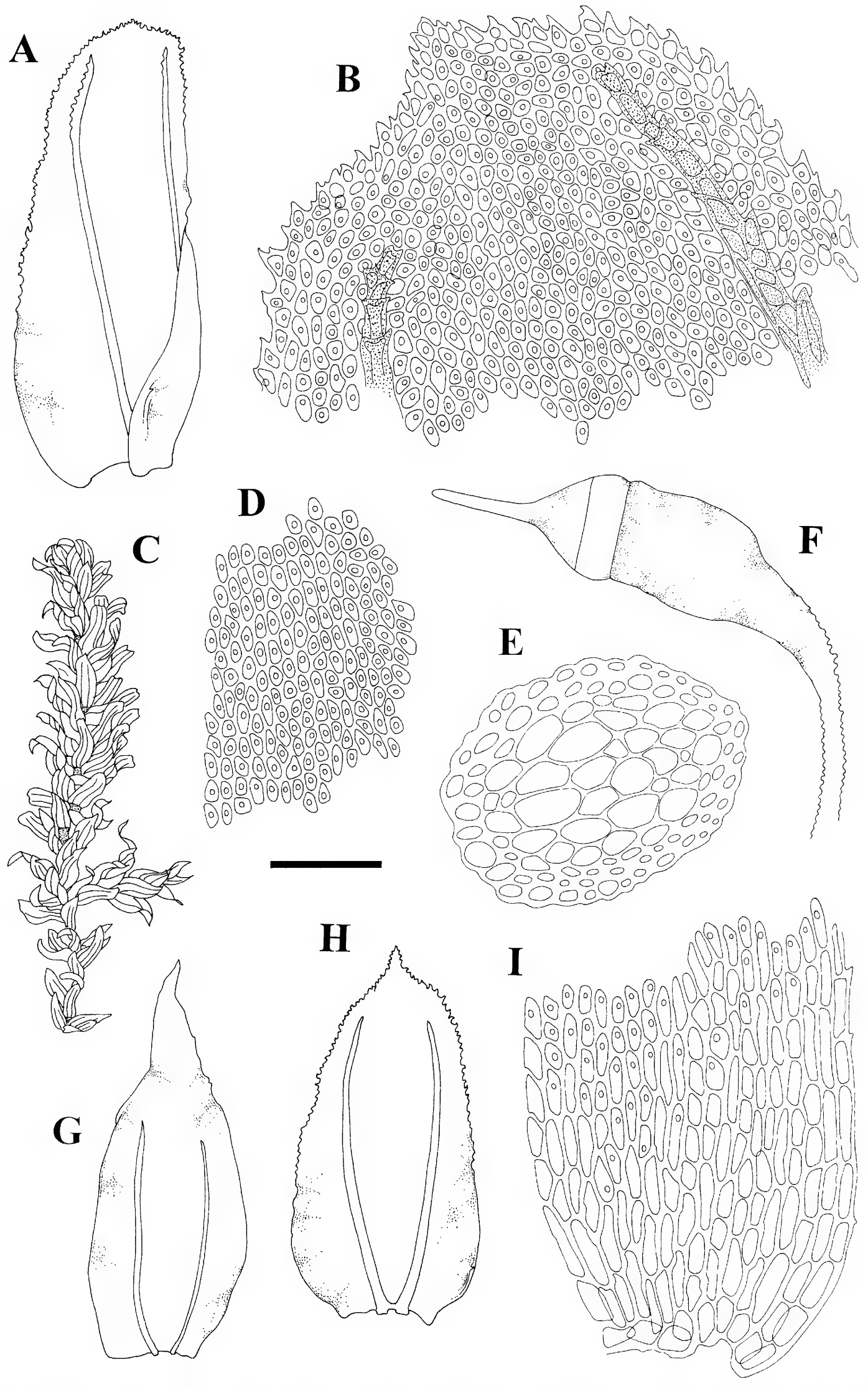


Figure 158. *Callicostella oerstediana*. A. Lateral leaf. B. Leaf apex. C. Habit. D. Median leaf cells between costae. E. Stem in cross section. F. Seta, capsule, annulus, and operculum. G. Ventral leaf. H. Dorsal leaf. I. Basal and alar cells. Scale in mm: bar = 0.06 (B, D, I); bar = 0.08 (E); bar = 0.28 (A, G, H); bar = 0.6 (F); bar = 1.56 (C). C from *Allen 15425*; F from *Croat 34239c*; all other figure parts from *Allen 18739*.

Plants small, 1.5–3.0 cm long, green, yellowish green, reddish yellow, or red, in dense or loose mats. Stems prostrate, subpinnately or irregularly branched, thick, hyaline to yellowish when young, becoming red with age; stems in cross section with epidermis of 1–3 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia subfoliose; axillary hairs 2 cells long, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves flexuose to inwardly subcrispate when dry, strongly dimorphic. Lateral and dorsal leaves wide-spreading, asymmetric or symmetric, ovate-lingulate to oblong-ovate, 0.8–1.4 mm long, rounded-obtuse to broadly acute, apiculate; margins irregularly erose-serrate in upper 2/3, subentire to entire below, plane throughout or plane below and narrowly recurved above on one side, rounded at base; costae double, strong, ending 7/8 the leaf length, diverging throughout, serrate or sharply toothed on back, projecting at the tips; upper cells unipapillose, papillae over the lumina, irregularly shaped, isodiametric, subhexagonal, or oval-hexagonal, 4–14 µm long, firm-walled, becoming larger toward the base, extreme basal cells short- to long-rectangular, 20–40 µm long, nonporose or occasionally porose; alar cells undifferentiated. Ventral leaves ovate-lanceolate, shortly acuminate, symmetric; margins irregularly dentate by swollen teeth in upper 2/3, plane; costae double, slender, often smooth at back, not or weakly projecting at the tips; upper cells lightly papillose to smooth, irregularly shaped, usually short-rectangular, but occasionally isodiametric or subhexagonal, thin-walled, becoming long-rectangular toward the base; alar cells undifferentiated. Autoicous or synoicous. Setae elongate, 7–13 mm long, orange when young, dark red with age, scabrous throughout. Capsules inclined to horizontal, symmetric and cylindric, neck well developed, 1.0 mm long; exothecial cells rounded-quadrate to oblong, incrassate, collenchymatous; stomata rudimentary, 3–5-celled, on neck; opercula conic-rostrate, 1.0 mm long; annuli massive, of 15–20 rows of thin-walled cells, separating from capsule along dehiscent zone at base, persistent on the operculum; peristome diplolepideous; exostome teeth narrowly triangular, with broad median furrows, densely and closely striate below, coarsely papillose above, dorsal surface dark red, ventral surface yellowish, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose, basal membranes high, segments broad, strongly keeled, not or weakly perforate, cilia absent. Spores rounded, 8–10 µm, smooth or lightly papillose. Calyptrae mitrate, fimbriate-laciniate to slenderly lobed at base, scabrous roughened above, naked, 2.0 mm long.

Illustrations. Welch (1966, Figs. 25–35); Sharp *et al.* (1994, Fig. 591 a–e). Figure 158.

Habitat. On rotting logs, stumps, or branches and tree trunks; 90–1400 m.

Distribution in Central America. BELIZE. Cayo: *Mains 3999* (FH, MO); Toledo: *Allen 18739* (BRH, MO). GUATEMALA. Alta Verapaz: *Cook & Griggs 388* (FH, NY, US); Izabal: *Kellerman 7397c* (US). HONDURAS. Cortés: *Standley et al. 7045* (F). COSTA RICA. Cartago: *Valerio 219* (FH, US); Limón: *Crosby 3689* (MO). PANAMA. Bocas del Toro: *Allen 5661A* (MO, PMA); Chiriquí: *Knapp & Vodicka 5573* (MO); Darién: *Folsom 6414B* (MO); Veraguas: *Croat 34239C* (MO).

World range: Mexico; Central America; Western South America.

Callicostella oerstediana is a common species in Central America, where it nearly always is found on rotting wood. It is a slender species, with stems that have a small sclerodermis and subfoliose pseudoparaphyllia. Its leaves are flexuose to inwardly subcrispate when dry and have irregularly erose-serrate to erose-dentate margins. Although the leaves exhibit remarkable dimorphism in correlation with their position on the stems, leaves of intermediate form are often present. The lateral and dorsal leaves are usually the largest, and they are typically broadly oblong, with rounded-obtuse, apiculate apices; very strong, often toothed costae; and small, irregularly shaped, strongly papillose leaf cells. The ventral leaves are ovate-lanceolate and shortly acuminate with upper margins irregularly dentate by swollen teeth. The costae in the ventral leaves are similar in length to those of the lateral and dorsal leaves, but they are thinner and often smooth on the dorsal surface. The ventral leaf cells are usually long and thin-walled, and they can be smooth or lightly papillose. Sporophytically, *C. oerstediana* has elongate setae that are scabrous throughout, strongly collenchymatous exothecial cells, and a massive annulus identical in form to that found in *Thamniopsis* and *Lepidopilum*.

In Central America *Callicostella oerstediana* is difficult to separate from *C. pallida*, which differs from it only in having evenly serrate rather than erose-serrate upper leaf margins. There is, however, a common Central American form of *C. pallida* that is extremely close to *C. oerstediana.* This form usually has leaves with tightly recurved, doubly serrate upper margins, and the marginal serrations are often large and bulging. These features give the leaf margins of *C. pallida* a ragged appearance that very closely approaches the erose-serrate margins of *C. oerstediana*. Both taxa also have stout, strongly bulging papillose leaf cells and costae that have either numerous sharp teeth or large, serrate crests. The two species may be synonymous. *Callicostella depressa* (Hedw.) A. Jaeger has been reported from Central America, but all collections with that name attached have turned out to be *C. oerstediana* or the common form of *C. pallida* that is close to it. *Callicostella depressa* is similar to *C. oerstediana* in having erose-serrate upper leaf margins. It differs, however, in having smooth setae and costae that end in large, multicellular, knob-like projections.

The isotype of *Callicostella oerstediana* in NY consists of only a few fragmented leaves, along with extensive notes on the type specimen at C. The leaves display all the features characteristic of *C. oerstediana*, as also do the notes on its sporophyte.

5. *Callicostella pallida* (Hornsch.) Ångstr., Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 33(4): 27. 1876. *Hookieria pallida* Hornsch. *in* Mart., Fl. Bras. 1(2): 64. 1840. *Schizomitrium pallidum* (Hornsch.) H. A. Crum & L. E. Anderson, Mosses E. N. Amer. 2: 822. 1981. Protologue. [Brazil] Epidendrum secundum flumen Amazonum et in Minis general. e.g. ad Villam Riccam: *Martius*; – ad truncos putridos silvarum umbrosarum prope Tijuca et alibi in prov. Rio de Janeiro, Octobri: *Beyrich et Olfers*.

Hookeria weigeltiana Müll. Hal., Linnaea 21: 190. 1848. *Callicostella weigeltiana* (Müll. Hal.) M. Fleisch., Hedwigia 63: 215. 1922. Protologue. [Suriname] Zuerst vom verstorbenen *Weigelt* in Surinam gesammelt.–An Baumstämmen bei *Paramáribo*. Hb. Kegel. Von den letzten beiden Standorten ohne No.

Hookeria cruceana Duby, Mém. Soc. Phys. Genève 19(2): 302. 1868. *Callicostella cruceana* (Duby) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 353. 1877. Protologue. [Mexico] Ad cortices arborum prope Vera-Cruz Mexicanorum detexit *D. Sumichrast*.

Callicostella subpallida Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 41(1): 87. 1904 [1905]. Protologue. Hab. Antilles: Portorico (*A. Heller*).

Hookeria tuberculosa Hampe *in* M. Fleisch., Hedwigia 63: 215. 1922, invalid name, lacks a description. *Callicostella tuberculosa* (Hampe) M. Fleisch., Hedwigia 63: 215. 1922. Based on *Hookeriopsis tuberculosa* Hampe, Costa Rica (FH).

Callicostella aquatica E. B. Bartram *in* B. Willis, Bryologist 42: 155. 1939. *Schizomitrium aquaticum* (E. B. Bartram) H. A. Crum, Bryologist 87: 208. 1984. Protologue. Panama. [Barro Colorado Island, Canal Zone, January and February 1938, *Barbara Willis*]. Types. Plants of Panama. On rock beneath water in brook starting about 30 m above Zetek trail. Barro Colorado Island, 21 Jan. 1939 [sic], *Barbara Willis 21* (FH, holotype); Mosses of Barro Colorado Island, Canal Zone, collected by *Barbara Willis*, January–February 1938 (F, isotype); Barro Colorado Island, Canal Zone, Jan-Feb. '38, coll. *Barbara Willis* (FH, isotype); Barro Colorado Island, Canal Zone. *Barbara Willis*, Collector, January–February, 1938 (US, isotype), *syn. nov*.

Plants small, 1.5–2.5(–5.0) cm long, green, yellowish green, reddish yellow, or red bronze, in dense or loose mats. Stems prostrate, subpinnately or irregularly branched, thick, hyaline to yellowish when young, becoming red with age; stems in cross section with epidermis of 1–3 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia subfoliose; axillary hairs 2 cells long, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves flexuose to inwardly subcrispate when dry, strongly dimorphic. Lateral and dorsal leaves wide-spreading, asymmetric or symmetric, ovate-lingulate to oblong-ovate, 0.8–1.4 mm long, rounded-obtuse to broadly acute, often apiculate; margins evenly single-serrate or coarsely double-serrate in upper 2/3, subentire to entire below, plane throughout or plane below and narrowly, tightly recurved above, rounded at base; costae double, strong, ending 7/8 the leaf length, diverging throughout, often sharply toothed to serrate-crested, occasionally nearly smooth, usually strongly projecting at the tips; upper cells strongly or weakly unipapillose, papillae over the lumina or prorate, irregularly shaped, isodiametric, subhexagonal, or

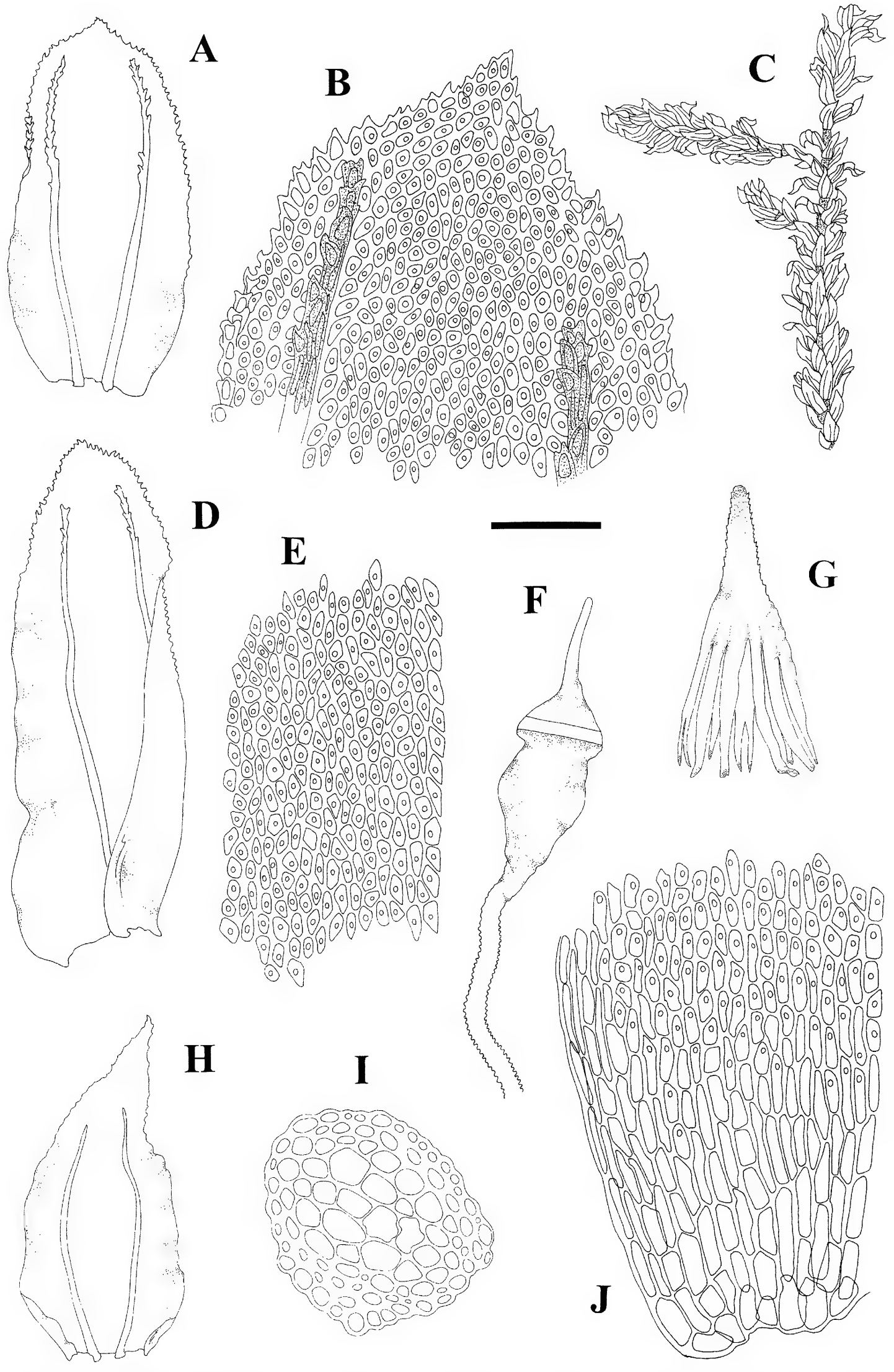
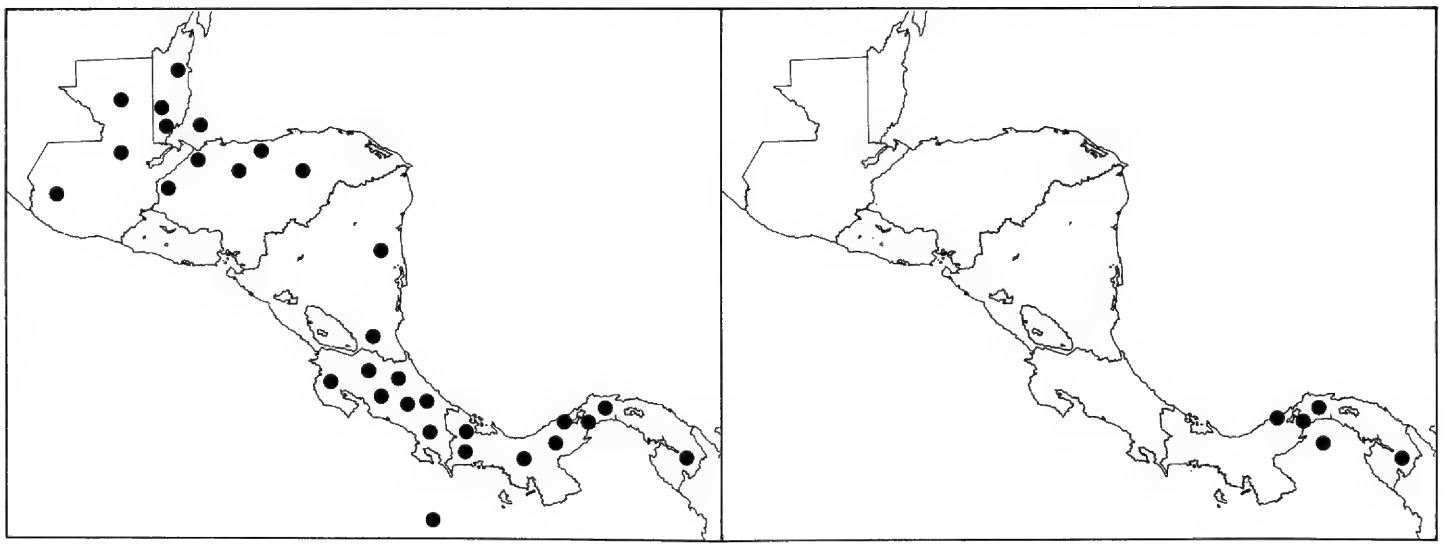


Figure 159. *Callicostella pallida*. A. Dorsal leaf. B. Leaf apex. C. Habit. D. Lateral leaf. E. Basal leaf cells between costae. F. Seta, capsule, annulus, and operculum. G. Calyptra. H. Ventral leaf. I. Stem in cross section. J. Basal and alar cells. Scale in mm: bar = 0.06 (B, E, J); bar = 0.08 (I); bar = 0.26 (A, D, H); bar = 0.6 (F); bar = 0.8 (G); bar = 1.56 (C). F, G from *Gentry & Burger 3003*; all other figure parts from *Antonio 5047G*.



Callicostella pallida *Callicostella rufescens*

oval-hexagonal, 4–14 µm long, firm-walled, becoming larger toward the base, extreme basal cells short- to long-rectangular, 20–40 µm long, nonporose or occasionally porose; alar cells undifferentiated. Ventral leaves ovate-lanceolate, plane; costae double, slender, often smooth at back, not or weakly projecting at the tips; upper cells lightly papillose to smooth, irregularly shaped, usually short-rectangular, but occasionally isodiametric or subhexagonal, thin-walled, becoming long-rectangular toward the base; alar cells undifferentiated. Autoicous or synoicous. Setae elongate, 10–16 mm long, orange when young, dark red with age, scabrous throughout or smooth below and roughened above near capsule. Capsules inclined, symmetric and cylindric, neck well developed, 1.0–1.5 mm long; exothecial cells rounded-quadrate to oblong, incrassate, collenchymatous; stomata rudimentary, 3–5-celled, on neck; opercula conic-rostrate, 1.0–1.5 mm long; annuli massive, of 10–12 rows of thin-walled cells, separating from capsule along dehiscent zone at base, persistent on the operculum; peristome diplolepideous; exostome teeth narrowly triangular, with broad median furrows, densely and closely striate below, coarsely papillose above, dorsal surface dark red, ventral surface hyaline to yellowish, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose, basal membranes high, segments broad, strongly keeled, not or weakly perforate, cilia absent. Spores rounded, 8–12 µm, smooth or lightly papillose. Calyptrae mitrate, fimbriate-laciniate to slenderly lobed at base, scabrous roughened above, naked, 1.5–2.0 mm long.

Illustrations. Duby (1868, Pl. 4 2); Grout (1934, Pl. 58 A, as *Callicostella scabriseta*); Willis (1939, Fig. 4 a–d); Bartram (1949, Fig. 134 F–I); Welch (1962, Figs. 16–23); Breen (1963, Pl. 103 5–9); Welch (1966, Figs. 36–46); Crum and Anderson (1981, Fig. 394 A–E); Reese (1984, Fig. 44 H & I); Florschütz-de Waard (1986, Fig. 124); Churchill (1994, Fig. 8 C–E); Sharp *et al.* (1994, Fig. 593); Churchill and Linares (1995, Fig. 35 f–j); Duarte Bello (1997, Pl. 254); Buck (1998, Pl. 23 9–18); Gradstein *et al.* (2001, Fig. 164 D–I); Buck (2003, Fig. 86); Vaz and Costa (2006a, Figs. 41–50). Figure 159.

Habitat. On rotting logs, tree trunks, branches, and rocks by or in streams, occasionally on top of bracket fungi; sea level–1800 m.

Distribution in Central America. BELIZE. Belize: *Allen 18000* (BRH, MO), Nicolas Cay: *Spellman & Stoddart B125C* (MO); Cayo: *Allen 15199* (MO); Toledo: *Allen 18649* (MO). GUATEMALA. Alta Verapaz: *Standley 91478* (F, FH, NY); Petén: *Bartlett 12598* (FH, NY, US); Quetzaltenango: *Standley 68229* (F, FH). HONDURAS. Atlántida: *Standley 55750* (F, FH, NY, US); Copán: *Blake 7465B* (NY, US); Cortés: *Morton 7750a* (US); Olancho: *Allen 12566* (MO); Yoro: *Allen 13596b* (MO). NICARAGUA. Río San Juan: *Smith* (FH); Zelaya: *Stevens 4889* (MO). COSTA RICA. Alajuela: *Gentry & Burger 3003* (MO); Cartago: *Crosby & Crosby 5787* (MO); Guanacaste: *Bowers 422* (MO); Heredia: *Gray 10001* (MO); Limón: *Standley 48523* (FH, NY, US); Puntarenas: *Dauphin 1614* (MO), Cocos Island: Weber *B-14302* (F, MO, NY, US); San José: *Skutch 2677* (FH, MO, NY, US). PANAMA. Bocas del Toro: *Allen 5651* (MO); Canal Area: *Nee 9421* (MO); Chiriquí: *McPherson 6824B* (MO); Coclé: *Salazar & Béliz 1355* (MO); Colón: *Crosby 10770* (MO); Darién: *Allen 8914* (MO); Panamá: *McDaniel 14257A* (F, MO, NY, PMA, US); Veraguas: *Taylor 1102* (FH).

World range: Southeastern U.S.A.; Mexico; Central America; Caribbean; Western and Northern South America, Brazil.

Callicostella pallida is the most commonly occurring species of the genus in Central America, where it typically grows on rotting wood. It is a slender species, with stems that have a small sclerodermis and subfoliose pseudoparaphyllia. Its leaves are flexuose to inwardly subcrispate when dry, and they exhibit remarkable dimorphism in correlation with their position on the stems. However, leaves of intermediate form are also commonly present. The lateral and dorsal leaves are usually the largest, and they are mostly broadly oblong with rounded-obtuse, apiculate apices, strong, often toothed, costae, and small, irregularly shaped, strongly papillose leaf cells. The ventral leaves are ovate-lanceolate and shortly acuminate, with upper margins irregularly dentate by swollen teeth. The costae in the ventral leaves are similar in length to those of the lateral and dorsal leaves, but they are thinner and often smooth on the dorsal surface. Furthermore, the ventral leaf cells are usually long and thin-walled, and they can be smooth or lightly papillose.

There are two distinctive forms of *C. pallida* in Central America. The most common form has leaves with usually doubly serrate upper margins. There is considerable variability in leaf margin form within leaves from single collections, but typically the margins are narrowly and tightly recurved and they have large, often bulging serrations. All these marginal features give the leaf margins a ragged appearance that very closely approximates those of *C. oerstediana*. This form has stout, strongly bulging papillose leaf cells and costae that have either numerous sharp teeth or large, serrate crests. It appears to represent the type concept as judged from illustrations of a syntype of *Hookeria pallida* (Welch 1962). The second form of the species has leaves with often broad apices, plane upper margins that have small, single marginal serrations, weakly papillose leaf cells, and costae that have weak or nearly absent dorsal serrations. This form of the species is typified in Central America by *C. aquatica*, and is also the form found in the southeastern United States.

Sporophytically, *C. pallida* has elongate setae that are usually scabrous throughout, but the setae can also be smooth below and roughened above near the capsule. Overall, variation in seta form is not correlated with either of the two vegetative forms of the species. However, all collections from Cocos Island have the common form of the gametophyte and setae that are consistently smooth below and rough above. The capsules in *C. pallida* have strongly collenchymatous exothecial cells and a massive annulus.

In Central America *Callicostella pallida* can be confused with *C. oerstediana* because the species have similarly shaped leaves with strongly papillose cells. *Callicostella oerstediana* differs from *C. pallida* only in having erose-serrate leaf margins. However, the variation in leaf margin form within *C. pallida* is so great that these species may eventually be considered synonymous. *Callicostella merkelii* could be confused with the *aquatica*-form of *C. pallida* because it has broadly rounded leaves and evenly serrate upper leaf margins. It differs from *C. pallida* in having smooth or weakly prorate upper leaf cells and double costae that strongly converge at the tips.

6. *Callicostella rufescens* (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 355. 1877. *Hookeria rufescens* Mitt., J. Linn. Soc., Bot. 12: 352. 1869. *Schizomitrium rufescens* (Mitt.) J. Florsch., Fl. Suriname 6(1): 328. 1986. Protologue. [Brazil and Suriname] Hab. Fl. Amazon, Pará ad ligna emortua, *Spruce, n. 629*; Surinam, *ex* Herb. Dozy. Type (see Florschütz-de Waard 1986). *Spruce 629*, Brazil, Pará (BM, lectotype).

Plants small, 1.0–3.0 cm long, green, yellowish green, reddish yellow, or red bronze, in dense or loose, glossy mats. Stems prostrate, irregularly branched, thick, dark red; stems in cross section with epidermis of 2–3 rows of small, very thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia subfoliose; axillary hairs 2 cells long, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves flexuose to inwardly contorted when dry, lateral leaves complanate-spreading, dorsal leaves erect when wet. Lateral and dorsal leaves asymmetric or symmetric, ovate, obovate, or oblong, 0.8–1.2 mm long, emarginate, truncate, rounded-obtuse or acute, at times apiculate; margins serrulate above, subentire to entire below, plane throughout or plane below and narrowly, tightly recurved

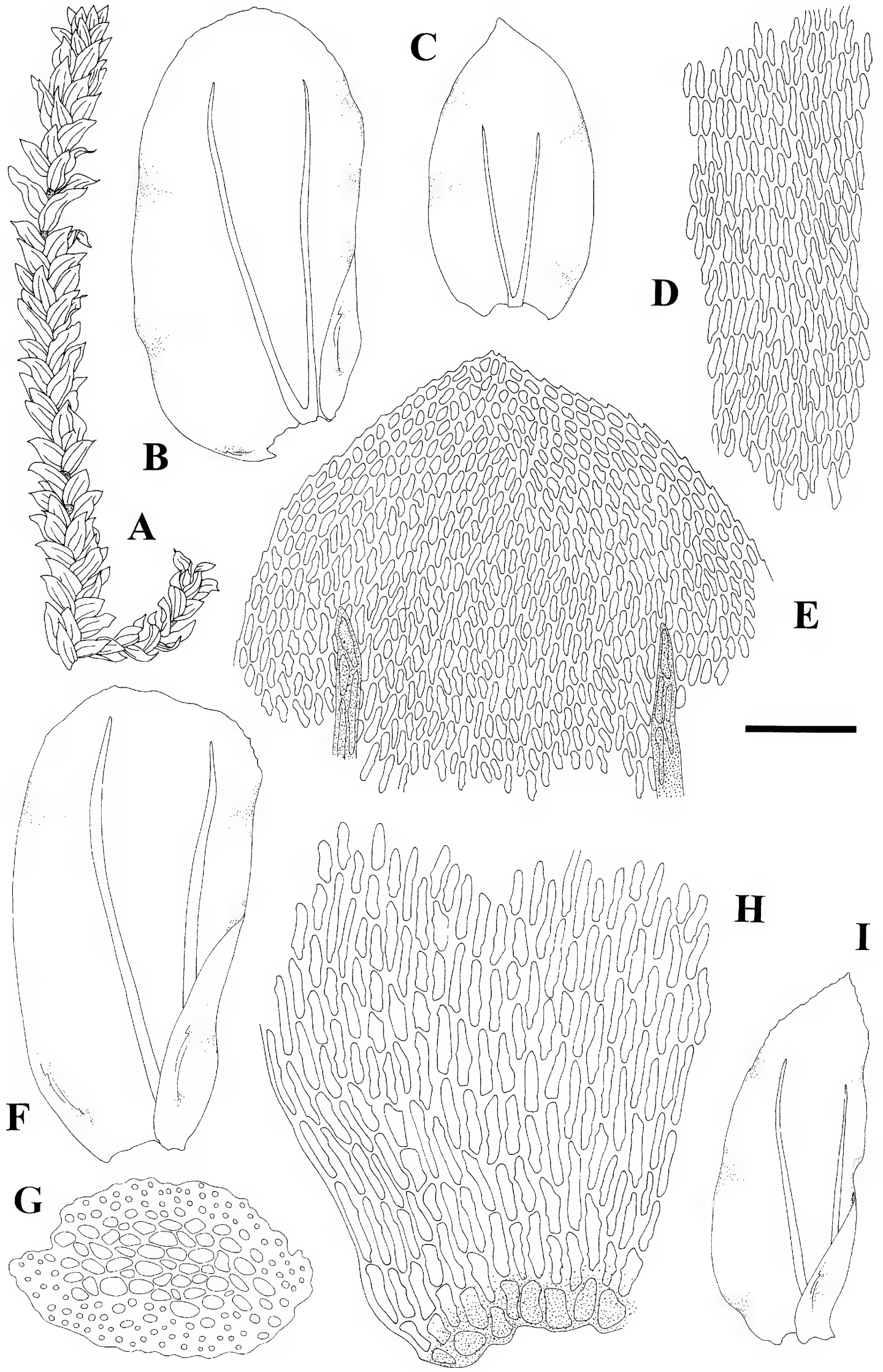


Figure 160. *Callicostella rufescens*. A. Habit. B & F. Lateral leaves. C & I. Dorsal leaves. D. Median leaf cells between costae. E. Leaf apex. G. Stem in cross section. H. Basal and alar cells. Scale in mm: bar = 0.06 (D, E, H); bar = 0.08 (G); bar = 0.26 (B, C, F, I); bar = 1.56 (A). A from *Crosby 4471*; all other figure parts from *Crosby 4325*.

above, rounded at base; costae double, strong, ending 7/8 the leaf length, diverging throughout or at times somewhat converging at the tips, smooth at back, usually projecting at the tips; cells smooth, firm-walled, often porose, upper cells long-hexagonal, oblong, or oblong-elongate, 10–20 × 4–6 µm, median cells oblong to oblong-elongate, basal cells subrectangular to rectangular, extreme basal cells long-rectangular, 30–40 µm long, smooth, porose, often yellowish across the insertions; alar cells undifferentiated. Ventral leaves 0.6–0.8 mm long, broadly ovate-lanceolate, shortly acuminate, symmetric; margins subentire, plane; costae double, slender, often smooth at back, not or weakly projecting at the tips; cells laxer and longer than those of lateral and dorsal leaves; alar cells undifferentiated. Dioicous or autoicous (?). Setae elongate, 9–12 mm long, orange to dark red, in Central America mostly smooth below and roughened above near capsule, occasionally scabrous throughout. Capsules inclined, symmetric and cylindric, neck well developed, 1.0 mm long; exothecial cells rounded-quadrate to oblong, incrassate, collenchymatous; stomata rudimentary, 3–5-celled, on neck; opercula conic-rostrate, 1.2 mm long; annulus not seen; peristome diplolepideous; exostome teeth narrowly triangular, with broad median furrows, densely and closely striate below, coarsely papillose above, dorsal surface dark red, ventral surface hyaline to yellowish, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose, basal membranes high, segments broad, strongly keeled, not or weakly perforate, cilia absent. Spores rounded, 10–16 µm, smooth or lightly papillose. Calyptrae mitrate, fimbriate-laciniate to slenderly lobed at base, scabrous roughened above, naked, 1.5–2.0 mm long.

Illustrations. Florschütz-de Waard (1986, Figs. 128 & 129); Buck (2003, Fig. 87); Vaz and Costa (2006a, Figs. 51–59). Figure 160.

Habitat. On bark of tree trunks, bases, or roots, rotting stumps or logs, and boulders along and in streams; 60–700 m.

Distribution in Central America. PANAMA. Canal Area: *Nee 11395* (MO, NY); Colón: *Crosby 10301* (MO, PMA); Darién: *Allen 8996* (MO); Panamá: *Crosby 4325* (F, FH, MO, NY, PMA, US), San José Island: *Johnston* (NY).

World range: Central America; Caribbean (Trinidad); Western and Northern South America, Brazil.

Callicostella rufescens is a South American species that is found in Central America only in eastern Panama, where it grows mostly on rotting logs or on bark at the base of trees. It occasionally is found on rocks and boulders. Although variable in color, plants of *C. rufescens* are usually reddish yellow to bronze. The species typically has complanate leaves and, in forms with well-spaced leaves, it has a *Neckeropsis*-like aspect. This aspect is enhanced by the presence of truncate to broadly rounded leaves. Leaf form in *C. rufescens*, however, is incredibly variable, and single stems can have leaves that range from emarginate to truncate or acute. The transition from one form to another on single stems occurs gradually. The lateral leaves of *C. rufescens* are usually the largest; they are somewhat asymmetric and ovate, obovate, or oblong in shape. Their margins are mostly plane, but here and there the upper margins can be narrowly recurved, and they are evenly serrulate above. The costae are strong, end near the apex, and except at the very tips are divergent throughout. The leaf cells of *C. rufescens* are the most distinguishing feature of the species and best separate it from all other Central American species of *Callicostella*. They are smooth throughout, incrassate, often porose, and consistently longer than narrow, varying from long-hexagonal to oblong-elongate above and long-rectangular at base. The distinctiveness of the long leaf cells in *C. rufescens* is best appreciated when comparing its median cells between the costae to those of the other Central American *Callicostella* species.

Although Central American collections of *C. rufescens* compare very well with South American material in terms of the leaf areolation, they differ in several ways. In South America the species is reported to be autoicous, synoicous, or dioicous, but I have seen no perigonia in Central American plants, and the species appears to be dioicous. South American plants are reported (Florschütz-de Waard 1986) to have generally more narrowly acute leaves, at times prorate upper leaf cells, and margins at times doubly serrate, with the teeth often enlarged. In addition, the setae are consistently scabrous throughout. Central American plants more often have truncate to broadly rounded leaf apices, the leaf cells are consistently smooth, and the upper leaf margins are always singly serrulate.

The setae in Central American collections are nearly always smooth below and lightly roughed above near the capsules. These differences seem important, and Central American material of this taxon may not be conspecific with *C. rufescens*. On the other hand, the areolation similarity between Central and South American material is so striking and the variability in leaf form within the species so great that the Central American material is here treated as *C. rufescens*.

In Central America *Callicostella rufescens* could be confused with *C. merkelii* because both species have broadly rounded leaf apices. *Callicostella merkelii*, however, has costae that are strongly convergent above, more or less isodiametric upper leaf cells, and shorter (hexagonal to rhombic) median cells between the costae.

Excluded taxa

Callicostella depressa (Hedw.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 352. 1877. *Leskea depressa* Hedw., Sp. Musc. Frond. 215. 1801. *Hypnum depressum* (Hedw.) Sw. *ex* P. Beauv., Prodr. Aethéogam. 63. 1805. *Hookeria depressa* (Hedw.) Hook. & Grev., Edinburgh J. Sci. 2: 231. 1825. *Pterygophyllum depressum* (Hedw.) Brid., Bryol. Univ. 2: 351. 1827. *Schizomitrium depressum* (Hedw.) W. R. Buck & Steere, Moscosoa 2: 47. 1983. Protologue. Jamaica, in lignis putrescentibus [*Swartz*]. Type. *Hypnum depressum* Swartz Prodr. b. a calyptra Portorico Persoon c a Brid. 28. d. minus a – (G, holotype).

Buck (1998) reported this species from Central America, but all Central American material so named is either the common Central American form of *C. pallida* or *C. oerstediana*. *Callicostella depressa* differs from both taxa in having costae that terminate in a projecting cluster of 3–6 spines. It is similar to *C. oerstediana* in having leaves with erose-serrate upper margins, but the two species differ in setae ornamentation: *C. depressa* has setae smooth throughout or smooth below and somewhat roughened near the capsule; *C. oerstediana* has setae scabrous throughout. The most common Central American form of *C. pallida* has leaves with usually doubly serrate, narrowly and tightly recurved upper margins that give the leaf margins a ragged appearance very similar to the erose-serrate margins of *C. depressa*. Sporophytically, *C. pallida* usually differs from *C. depressa* in having setae that are scabrous throughout, but there are some collections of *C. pallida* (especially those from Cocos Island) with setae that are smooth below and roughened above near the capsule.

5. *Crossomitrium* Müll. Hal., Linnaea 38: 611. 1874.

Plants small or medium-sized, forming dense or thin, glossy, yellowish green (occasionally reddish yellow) mats. Stems creeping, usually tightly adhering to the substrate, irregularly pinnately branched, cells elongate-rectangular (except for discoid areas of quadrate cells just below the junction of the leaf and stem); stems in cross section with outer layer of small, firm-walled cells, cortical cells enlarged, thin-walled, central strand absent; pseudoparaphyllia and paraphyllia absent; axillary hairs 2(–3)-celled, basal cell quadrate, red brown, upper cell(s) elongate-oblong, hyaline; rhizoids restricted to the substrate side of stems, reddish brown, smooth, not or sparsely branched, from clusters of initials abaxial to leaf insertions and from contiguous basal leaf cells. Leaves in four rows, variously dimorphic (lateral leaves and ventral/dorsal leaves), usually complanate-foliate; apices acute to acuminate, frequently carinate; margins uni- or biserrate to bidentate by projecting end walls, plane or recurved, marginal cells with 1–4 low papillae over the lumina, otherwise cells smooth; costa none; upper and median cells linear to elongate-rhomboidal; basal median cells enlarged, hexagonal to pentagonal; alar cells not differentiated. Asexual reproduction by elongate, uniseriate, multicellular brood bodies originating from rhizoidal initials on stems and leaf bases and on specialized brood branches. Dioicous. Perigonia and perichaetia sessile along branches and stems. Setae elongate, red to red brown, smooth below and papillose above or scabrose throughout (occasionally smooth throughout). Capsules suberect to inclined, ovoid to elliptic; exothecial cells short-rectangular, collenchymatous; stomata on neck, stomatal guard cells often irregularly secondarily divided; opercula shortly conic-rostrate; annuli persistent, of 3–4 layers of quadrate, thin-walled cells; peristome diplolepideous; exostome teeth 16, yellowish white, hydrocastique, papillose throughout, dorsal and ventral trabeculae weakly projecting; endostome longer than exostome teeth, white to yellowish, pa-

pillose, basal membranes high or low, segments keeled, variously perforate, cilia absent. Calyptrae mitrate, smooth to roughened above, fimbriate at base by uniseriate, multicellular hairs.

Crossomitrium is a genus of six species endemic to the New World and nearly restricted to the tropics. It is one of the few mosses that grows consistently, indeed characteristically, on leaves. Plants of *Crossomitrium* often tightly adhere to the substrate and are irregularly pinnately branched. The species of *Crossomitrium* are remarkably consistent in many of their features. Its stems lack a central strand, paraphyllia, and pseudoparaphyllia. Rhizoids are produced from clusters of initials on the stems abaxial to the leaf insertions and from enlarged nematogen cells at the middle of the leaves near the insertion lines. *Crossomitrium* has 2-celled (occasionally 3-celled) axillary hairs consisting of a small, quadrate, reddish brown basal cell and a hyaline, subglobose terminal cell. The leaves of *Crossomitrium* are dimorphic and often the apex is carinate. The leaf cells are linear-flexuose except at the extreme base, where there is a small, circular group of short, enlarged, and sometimes bulging cells in the middle of the leaf. The leaves have undifferentiated alar cells and are absolutely ecostate. The marginal rows of leaf cells have one to many papillae and are always doubly serrate by the projecting cell end walls; otherwise the leaf cells are smooth. All species (and nearly all collections) of *Crossomitrium* reproduce asexually by means of stalked, uniseriate, multicellular brood bodies that occur abaxial to the ventral leaves or on specialized brood branches.

Despite its dioicous sexual condition and epiphyllous habitat, sporophytes are fairly often encountered in *Crossomitrium*. The sporophytes of *Crossomitrium* have long setae, suberect, ovoid to elliptic, usually symmetric capsules, with collenchymatous exothecial cells, secondarily divided stomatal guard cells, and conic-rostrate opercula. *Crossomitrium* has a diplolepideous peristome with yellowish white exostome teeth that are papillose throughout on both surfaces. The teeth are hygrocastique: recurved when wet, erect or incurved when dry. The endostomes can have high or low basal membranes; well-formed, keeled segments; and no cilia. The calyptrae are one of the oddest features of *Crossomitrium*. They are mitrate and densely ciliate-fringed at base, with hairs arising from the marginal cells. This type of calyptra is also seen in the Daltoniaceae as well as some species of *Campylopus*. However, unlike those other fringed calyptrae, the calyptral hairs in *Crossomitrium* are uniseriate and multicellular, with short, quadrate cells.

Crossomitrium has sometimes been placed in the Daltoniaceae because of its hydrocastique peristome, fringed calyptrae, and collenchymatous exothecial cells. The genus, however, is better placed in the Hookeriaceae on the basis of five characters: (1) branched stems; (2) ecostate leaves; (3) straight, unbranched rhizoids that are tightly clustered abaxial to the leaf insertions; (4) two-celled axillary hairs; and (5) weakly pigmented stems. The genus was revised by Allen (1990).

The name *Crossomitrium* combines the Greek *krossos* (a fringe or tassel) and *mitria* (cap) and refers to the fringed calyptra of the genus.

1. Setae spinose to scabrose throughout 2
1. Setae smooth in lower 2/3 and papillose to scabrose in upper 1/3 OR setae absent. 3

2. Leaf margins dentate and strongly recurved throughout . . . . . 1. *C. acuminatum*
2. Leaf margins serrate to serrulate and plane to weakly recurved at the middle . . . . . 6. *C. scabrisetum*

3. Lateral leaves less than 1.2 mm long 4
3. Lateral leaves greater than 1.3 mm long, often more than 1.5 mm long 6

4. Lateral leaves lanceolate-oblong, erect at base then arching downward to the substrate; brood branches tightly adhering to the substrate; brood leaves closely spaced and rigidly overlapping . . . . . 3. *C. patrisiae*
4. Lateral leaves oval-acute, flattened to the substrate; brood branches erect and free from the substrate; brood leaves loosely spreading on all sides 5

5. Brood bodies clustered at apex of the brood branches. . . . . 5. *C. saprophilum*
5. Brood bodies borne along the length of the brood branches . . . . . 2. *C. epiphyllum*

6. Leaf margins dentate and strongly recurved throughout . . . . . 1. *C. acuminatum*
6. Leaf margins serrate to serrulate and plane to weakly recurved at the middle 7

7. Lateral leaves with parallel sides, widest below the middle; commonly with specialized brood branches tightly adhering to the substrate . . . . . 3. *C. patrisiae*
7. Lateral leaves with convex sides, widest above the middle; specialized brood branches absent . . . . . 4. *C. rotundifolium*

1. *Crossomitrium acuminatum* E. B. Bartram, Rev. Bryol. Lichénol. 22: 157. 1953. Protologue. Panama. Westerly arm of Quebrada, Salamanca, Canal Zone, 70 m, *C. W. Dodge, J. A. Steyermark & P. H. Allen*, Dec. 16, 1934. Type. Panama. Plants of the Canal Zone and adjacent Panama. Westerly arm of Quebrada Salamanca, 70 m, *C. W. Dodge, J. A. Steyermark* and *P. H. Allen*, December 16, 1934 (FH, holotype; MO, isotype).

Plants slender to medium-sized, 1–4 cm long, glossy, yellowish green. Stems prostrate, irregularly pinnately branched, reddish brown, usually complanate-foliate; cross section of stems with epidermis of 1–2 rows of small, thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2 cells long, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions and from contiguous basal leaf cells, smooth, reddish brown, unbranched below and with short branches at point of contact with substrate. Leaves in four rows, dimorphic. Lateral leaves erect at base and arching downward toward the substrate above, frequently overlapping at base, oblong to oblong-lanceolate, 1–2 × 0.3–0.5 mm, with nearly parallel sides, short-acuminate to acute, often carinate at apices. Dorsal leaves shorter and broader, subovate, erect-spreading when dry; margins sharply and coarsely doubly dentate by projecting cell end walls, teeth frequently recurved, tightly and narrowly recurved for most of the leaf length, marginal cells often with 1 or more papillae; costa none; upper and median cells linear to vermicular, 60–160 × 3–5 µm, firm-walled; basal cells near insertions 30–60 × 12–35 µm; alar cells undifferentiated. Asexual reproduction by brood bodies borne abaxial to the ventral leaf insertions or on specialized julaceous branches adnate to the substrate; brood leaves imbricate, orbicular, apiculate, cordate at base; brood bodies uniseriate, multicellular, 2 or more from a uniseriate, multicellular stalk. Dioicous. Perigonia and perichaetia sessile along stems and branches. Setae elongate, 5 mm long, red to red brown, scabrose to tuberculose throughout. Capsules inclined, ovoid to elliptic, neck moderately developed, 1.0 mm long; exothecial cells short-rectangular, collenchymatous; stomata on neck; opercula conic-rostrate, 0.7 mm long; annuli rudimentary; peristome diplolepideous; exostome teeth yellowish white, recurved when wet, incurved when dry (hydrocastique), narrowly triangular, both surfaces papillose throughout, dorsal trabeculae and median lines weak, ventral trabeculae moderately developed; endostome yellowish white, spiculose-papillose above, basal membranes low, segments linear, keeled, not or faintly perforate, cilia absent. Spores rounded, 10–13 µm, lightly papillose. Calyptra not seen.

Illustrations. Welch (1974, Figs. 73–78); Allen (1990, Figs. 2–4); Churchill and Linares (1995, Fig. 37 a–d). Figure 161.

Habitat. On leaves; sea level to 1650 m.

Distribution in Central America. NICARAGUA. Zelaya: *Stevens 6945* (MO). PANAMA. Bocas del Toro: *Allen 5582* (CANM, MO, NY); Canal Area: *Dodge 17018* (MO); Veraguas: *Crosby 10163* (MO, PMA).

World range: Central America; Western South America.

Crossomitrium acuminatum is a moderately sized species with lanceolate-oblong lateral leaves. The lateral leaves are similar in shape to those of *C. patrisiae*, and both species have the same leaf stance when dry: erect at base and arching downward toward the substrate in the upper part. These species also have specialized brood branches that are adnate to the substrate and similar in form. The two species, however, differ gametophytically and sporophytically. In *C. patrisiae* the leaf margins are serrate rather than dentate and either plane or weakly recurved at the middle of the leaf. The presence of setae that are scabrose to tuberculose throughout distinguishes *C. acuminatum* from *C. patrisiae*, which has setae that are smooth below.

Crossomitrium scabrisetum is similar to *C. acuminatum* in having entirely scabrose to tuberculose setae. It differs from *C. acuminatum* in having serrate rather than dentate leaf margins that are ei-

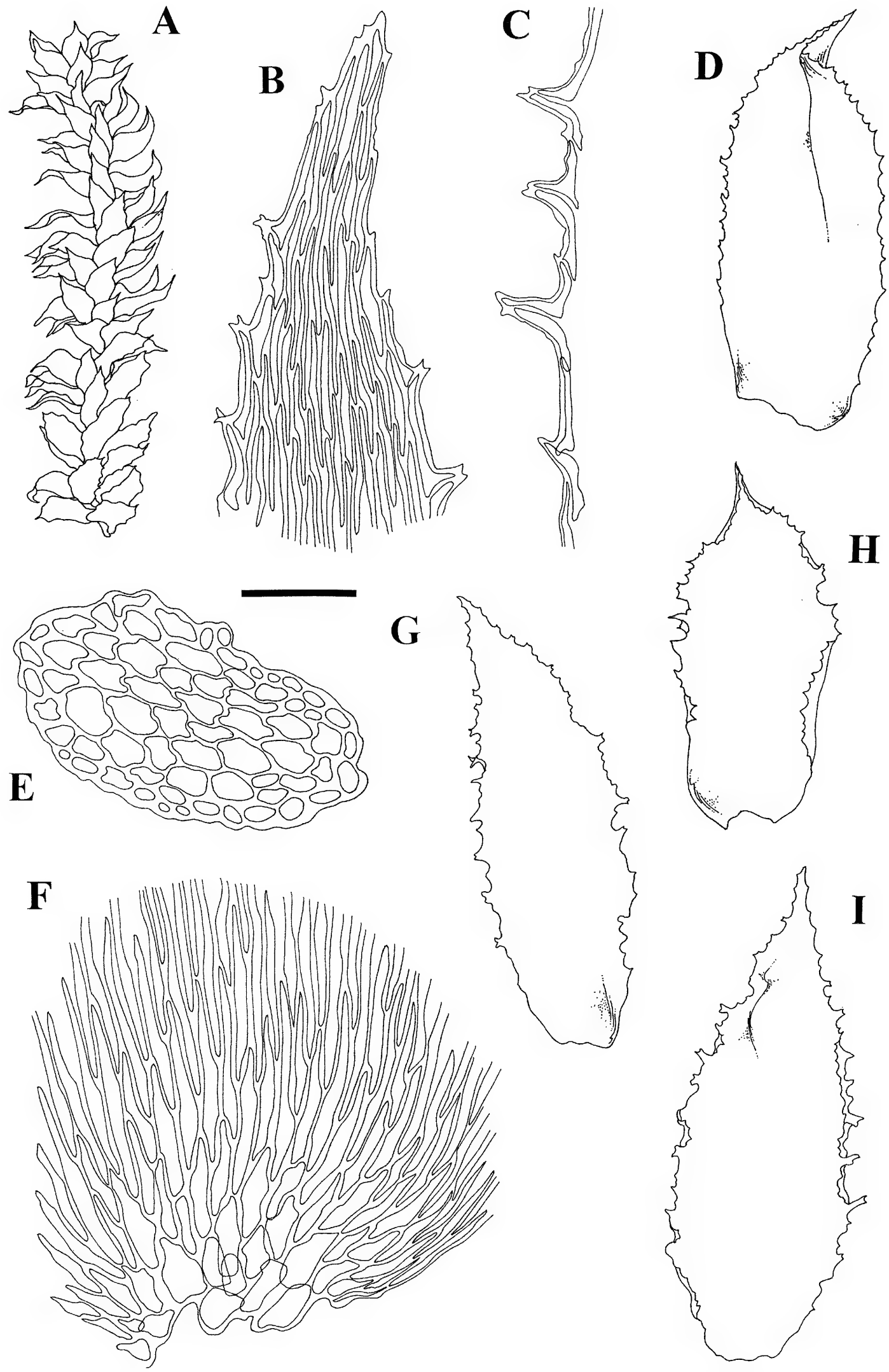
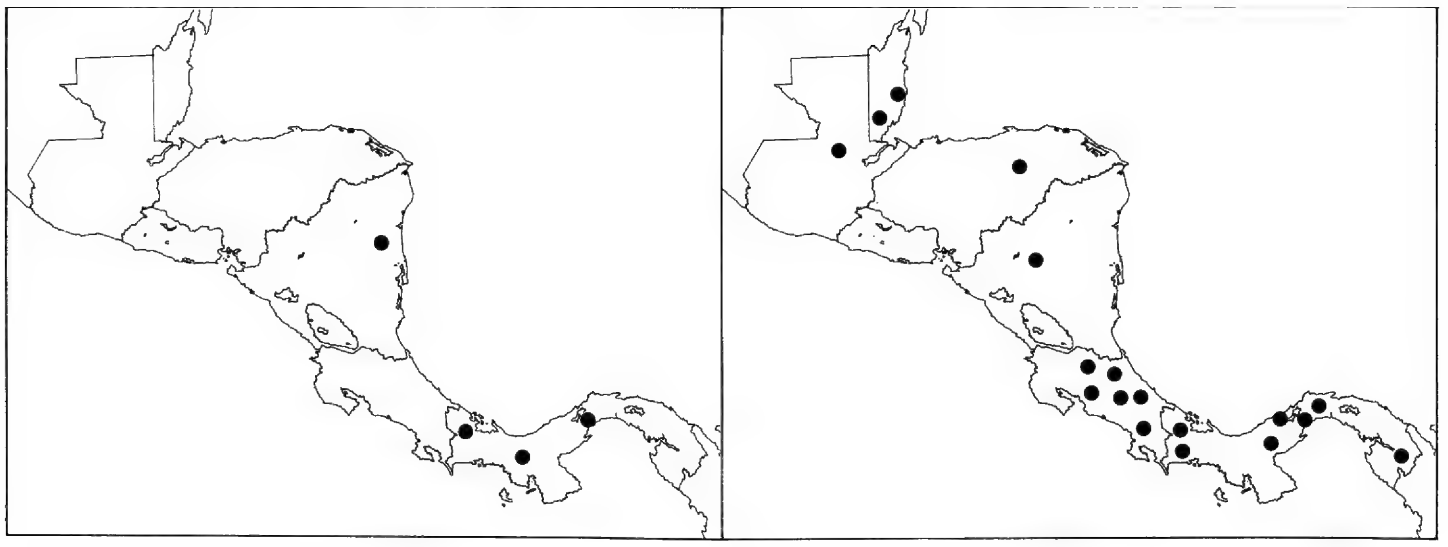


Figure 161. *Crossomitrium acuminatum*. A. Habit. B. Leaf apex. C. Upper leaf margin. D, G–I. Leaves. E. Stem in cross section. F. Basal and alar cells. Scale in mm: bar = 0.05 (E); bar = 0.06 (B, C, F); bar = 0.28 (D, G–I); bar = 1.56 (A). B, F from *Dodge et al.* (type); G, I from *Cuatrecasas 26039B*; all other figure parts from *Allen 5582*.



Crossomitrium acuminatum *Crossomitrium epiphyllum*

ther plane or weakly recurved at the middle of the leaf. Although *C. epiphyllum* and *C. saprophilum* are similar in size to *C. acuminatum*, both species have broadly oval to orbicular leaves and erect rather than adnate brood branches.

2. *Crossomitrium epiphyllum* (Mitt.) Müll. Hal., Linnaea 38: 613. 1874. *Lepidopilum epiphyllum* Mitt., J. Linn. Soc., Bot. 12: 370. 1869. Protologue. [Ecuador] Andes Quitenses, in sylva Canelos (3000 ped.), *Spruce, n. 800*; Chimborazo (3000 ped.), ad folia, *Spruce, n. 801*. Types (see Allen 1990). Chimborazo, ad folia, *Spruce 801* (NY, lectotype; S, isolectotype). Andes Quitenses, in sylva Canelos, *Spruce 800* (NY, syntype).

Crossomitrium oerstedianum Müll. Hal., Flora 58: 545. 1875. Protologue. Patria. Costa Rica, 5000–8000 ped. altum: *A. F. Oersted* in folio coriaceo legit. Type. Costa Rica, in folio coriaceo, *Oersted s.n.* (FH, isotype).

Lepidopilum flaccidissimum Besch. *ex* Kindb., Enum Bryin. Exot., Suppl. 2: 100. 1891, invalid name, lacks a description. Based on Guadeloupe, *Marie 175* (NY).

Crossomitrium orbiculatum Müll. Hal., Hedwigia 37: 244. 1898. Protologue. Portorico, prope Adjuntas in montibus, Majo 1886: *P. Sintenis* in Hb. Krug et Urban. Types (see Welch 1971b). Holotype destroyed. Puerto Rico, N slope of Luquillo Mts., on stump, March 8, 1899, *Heller & Heller 796* (NY, neotype; BM, MICH, isoneotypes).

Lepidopilum calomicron Broth. *in* Urb., Symb. Antill. 3: 426. 1903. *Crossomitrium calomicron* (Broth.) W. H. Welch, Bryologist 74: 89. 1971. Protologue. Hab. in Martinique in Morne Rouge, ad folia arborum: *Duss n. 352* (in Herb. Berol.). Types (see Allen 1990). Martinique in Morne Rouge, ad folia arborum: *Duss n. 352* (H, lectotype; NY, isotype).

Crossomitrium cubense P. de la Varde & Thér. *in* Thér., Mem. Soc. Cub. Hist. Nat. "Felipe Poey" 14: 370. 1940. Protologue. [Cuba] Loma San Juan, epiphyte, leg. *Hioram No. 13748*. Types. Cuba: Guantanamo, Loma San Juan, 1100 m, *Hioram 13748* (PC, holotype; JE, isotype). Cuba. Loma del Gato, Sierra Maestra (Oriente), *Hioram 13748* (FH, NY, isotypes).

Plants small, 1–7 cm long, glossy, yellowish green. Stems prostrate, irregularly pinnately branched, reddish brown, usually complanate-foliate; cross section of stems with epidermis of 1–2 rows of small, thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2 cells long, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions and from contiguous basal leaf cells, smooth, reddish brown, unbranched below, with short branches at point of contact with substrate. Leaves in four rows, dimorphic. Lateral leaves flattened to the substrate and overlapping with leaf above, or erect-spreading, obovate, orbicular, oval, or sub-oblong, 0.5–1.0(–1.2) mm long, with convex sides widest above the middle, acute to shortly apiculate. Dorsal leaves shorter and broader, orbicular, flattened to the stems when dry; margins weakly doubly serrate by projecting cell end walls at base, plane, marginal cells often with 1 or more papillae; costa none; upper and median cells linear to vermicular, 50–150 × 5–10 µm, firm-walled; basal cells near insertions 50–70 × 18 µm; alar cells undifferentiated. Asexual reproduction by brood bodies borne

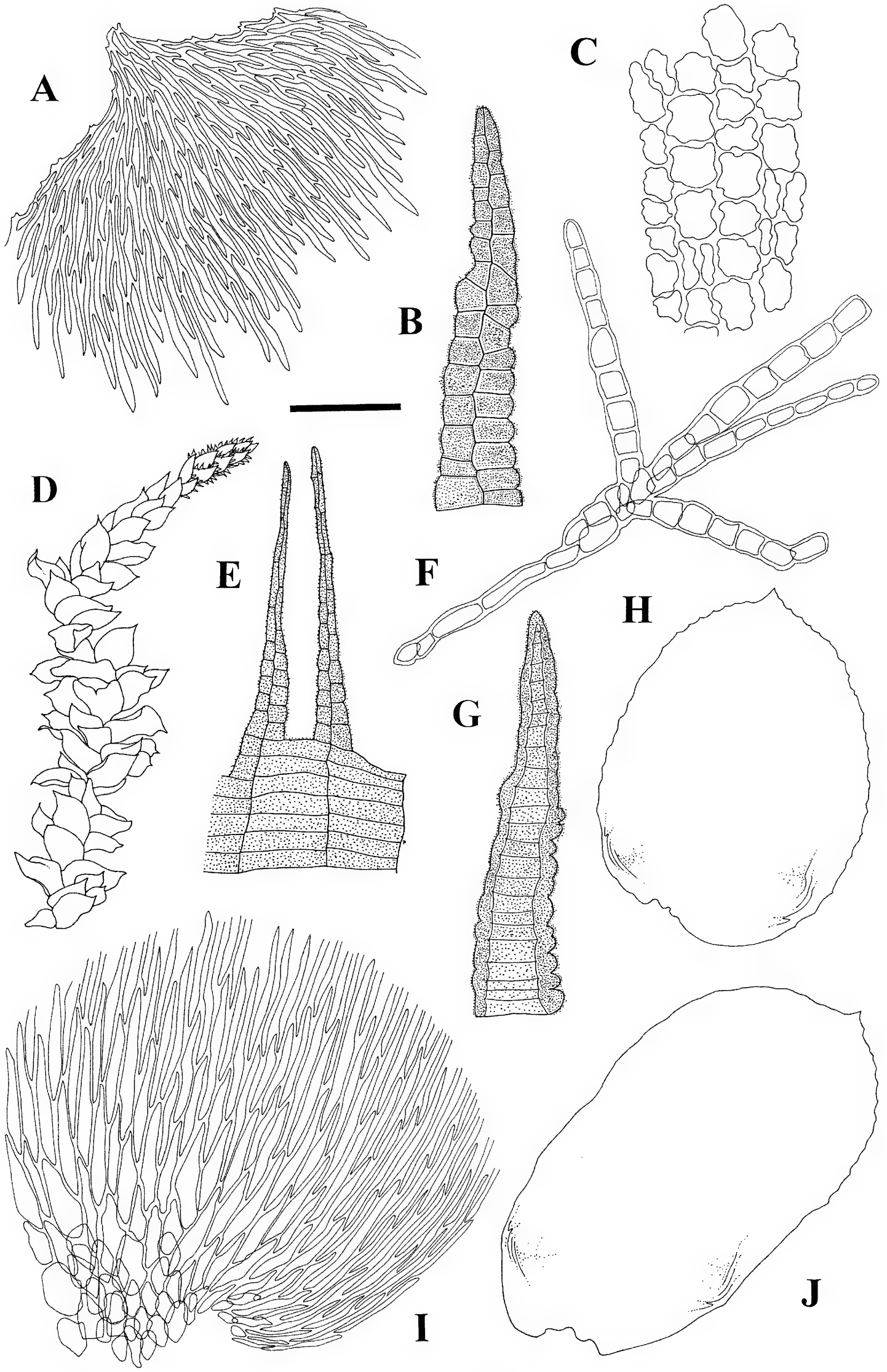


Figure 162. *Crossomitrium epiphyllum*. A. Leaf apex. B. Exostome, dorsal (outer) surface. C. Exothecial cells. D. Habit. E. Endostome, dorsal (outer) surface. F. Gemmae. G. Exostome, ventral (inner) surface. H & J. Leaves. I. Basal and alar cells. Scale in mm: bar = 0.06 (A, C, I); bar = 0.13 (F); bar = 0.28 (H, J); bar = 1.0 (B, E, G); bar = 1.56 (D). B, C, E, G from *Buck 10562*; D from *Allen 15456*; all other figure parts from *Spruce 801* (type).

abaxial to the ventral leaf insertions or on specialized erect branches; brood leaves erect-spreading from all sides or moderately flattened, oval to orbicular, apiculate, cordate at base; brood bodies uniseriate, multicellular, 2 or more from a uniseriate, multicellular stalk. Dioicous. Perigonia and perichaetia sessile along stems and branches. Setae elongate, 4–7 mm long, red to red brown, papillose above, smooth below. Capsules inclined to suberect, ovoid to elliptic, neck moderately developed, 0.7–1.0 mm long; exothecial cells short-rectangular, collenchymatous; stomata on neck; opercula conic-rostrate, 1 mm long; annuli rudimentary; peristome diplolepideous; exostome teeth yellowish white, occasionally with light reddish tint, recurved when wet, incurved when dry (hydrocastique), narrowly triangular, both surfaces papillose throughout, dorsal trabeculae and median lines weak, ventral trabeculae moderately developed; endostome yellowish white, spiculose-papillose above, basal membranes high, segments linear, weakly keeled, not or faintly perforate, cilia absent. Spores 10–13 µm, lightly papillose. Calyptrae mitrate, reddish brown, roughened above and fimbriate at base, 1.0–1.5 mm long.

Illustrations. Thériot (1940, Pl. 55 9 a–e); Bartram (1949, Fig. 142 I–K); Welch (1969, Figs. 24–31); Welch (1971b, Figs. 72–95); Welch (1974, Figs. 79–85); Allen (1990, Figs. 24–32, 34, 36–38); Churchill and Linares (1995, Fig. 37 e–g); Duarte Bello (1997, Pl. 224); Buck (1998, Pl. 17 1–6); Buck (2003, Fig. 88 A–F). Figure 162.

Habitat. On leaves, twigs, tree branches and trunks, rotting logs, stumps, and boulders; 100–2340 m.

Distribution in Central America. BELIZE. Stann Creek: *Townsend 94/276* (MO); Toledo: *Allen 15456* (MO). GUATEMALA. Alta Verapaz: *Standley 70967* (FH). HONDURAS. Olancho: *Allen 12581* (MO). NICARAGUA. Matagalpa: *Stevens 22726* (HNMN, MO). COSTA RICA. Alajuela: *Holm et al. 1312* (G); Cartago: *Crosby & Crosby 8554* (CR, MO); Heredia: *Bowers* (MO); Limón: *Daly 103* (MO); Puntarenas: *Liesner 1788* (MO); San José: *Crosby & Crosby 5870* (CR, MO). PANAMA. Bocas del Toro: *Allen 5582 p.p.* (MO, filed under *Crossomitrium acuminatum*); Canal Area: *Meyer 149* (MICH); Chiriquí: *Crosby 4048b* (MO); Coclé: *Luer et al. 10646* (MO); Colón: *Crosby 10773* (MO, PMA); Darién: *Allen 9015c* (MO); Panamá: *Crosby 7213* (MO, PMA).

World range: Central America; Caribbean; Western and Northern South America.

Crossomitrium epiphyllum is a commonly encountered species, with a range nearly equal to that of the genus. It is generally found at higher elevations than *C. patrisiae*, which is more common in the lowland tropics, but they often occur together on the same leaf or twig. In its typical expression, *C. epiphyllum* is distinguished from *C. patrisiae* (as well as *C. scabrisetum* and *C. acuminatum*) by its strongly flattened, obovate to orbicular lateral leaves that are less than 1.0 mm long. *Crossomitrium patrisiae* has arching, lanceolate-oblong lateral leaves that are greater than 1.2 mm long. In addition, the brood bodies of *C. patrisiae* are adnate to the surface rather than erect and have imbricate leaves. When sporophytes are present, the two species can be separated by examining the endostomial basal membrane. In *C. epiphyllum* it is more than one-third, while in *C. patrisiae* it is one-quarter or less the height of the endostome. There is a troublesome expression of *C. epiphyllum* (nomenclaturally centered on *C. calomicron*) with oblong, erect to erect-spreading lateral leaves that grades closely into *C. patrisiae.* These *calomicron*-forms can sometimes only be recognized by the presence of horizontal to erect, rather than adnate brood branches.

Crossomitrium saprophilum is gametophytically identical to some expressions of *C. epiphyllum*. The two species differ only in the way propagula are borne on the erect brood branches. In *C. epiphyllum* they occur along the length of the brood branches, while in *C. saprophilum* they are found in a massive terminal cluster. *Crossomitrium rotundifolium* is a considerably larger species than *C. epiphyllum*, with leaves that are 1.3–2.0 mm long. In addition, *C. rotundifolium* lacks specialized brood branches and the propagula are borne in large, dense clusters along the stems and branches.

3. *Crossomitrium patrisiae* (Brid.) Müll. Hal., Linnaea 38: 612. 1874. *Hypnum patrisiae* Brid., Bryol. Univ. 2: 539. 1827. *Hookeria patrisiae* (Brid.) Hampe, Icon. Musc. 1. 1844. *Lepidopilum patrisiae* (Brid.) Mitt., J. Linn. Soc., Bot. 12: 369. 1869. Protologue. [French Guiana] In Cayennae arboribus praesertim in Patrisiâ pyriferâ. Clariss. *Fee* assueta humanitate communicavit. Type. French Guiana, Cayenne in foliis Patrisiae pyriferae, *Fée s.n.* (B, holotype).

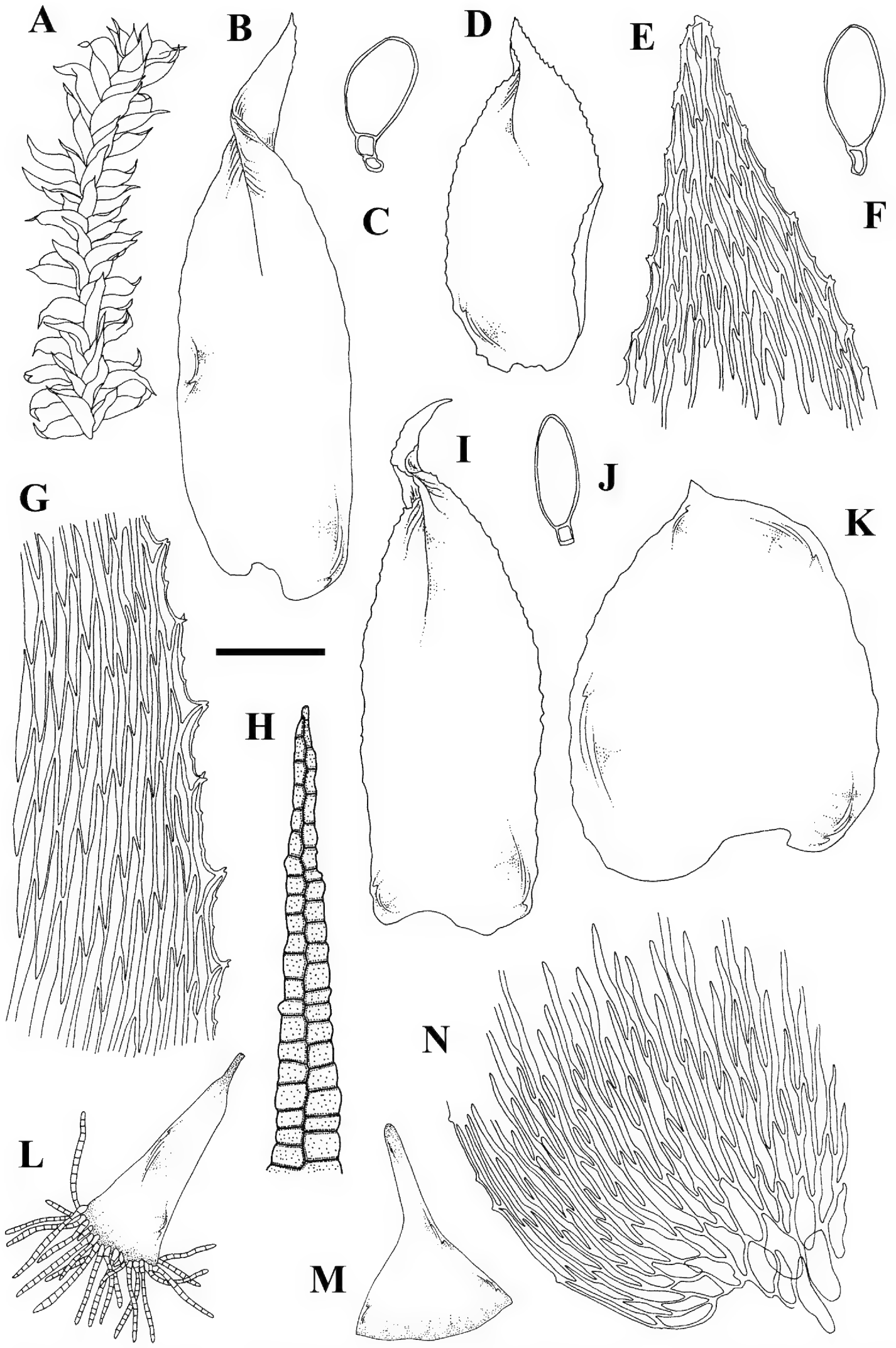
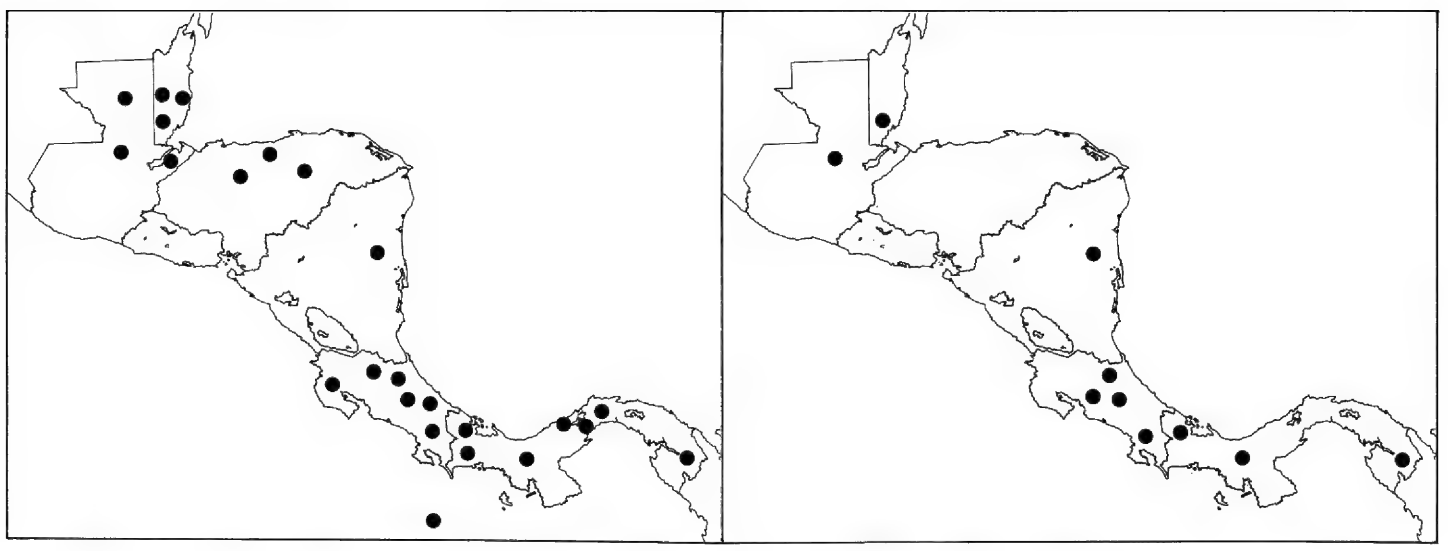


Figure 163. *Crossomitrium patrisiae*. A. Habit. B, D & I. Leaves. C, F & J. Axillary hairs. E. Leaf apex. G. Median leaf cells and margin. H. Exostome, dorsal (outer) surface. K. Leaf subtending gemmae. L. Calyptra. M. Operculum. N. Basal and alar cells. Scale in mm: bar = 0.05 (C, F, J); bar = 0.06 (E, G, N); bar = 0.09 (H); bar = 0.28 (B, D, I, K); bar = 0.36 (L); bar = 0.5 (M); bar = 2.5 (A). B, D, E, I, K, N from *Fée* (type); G from *Buck 10370*; H from *Ule 263*; M from *Buck 3177*; all other figure parts from *Allen 8815*.



Crossomitrium patrisiae *Crossomitrium rotundifolium*

Hookeria splitgerberi Mont., Syll. Gen. Sp. Crypt. 14. 1856. *Lepidopilum splitgerberi* (Mont.) Mitt., J. Linn. Soc., Bot. 12: 370. 1869. *Crossomitrium splitgerberi* (Mont.) Müll. Hal., Linnaea 38: 613. 1874. Protologue. [Suriname] In folio coriaceo ad Surinam lecto hancce [hanc] speciem ab omnibus congeneribus distinctissimam legit *SPLITGERBER* qui mecum sub *n° 1205*, dum vivebat, communicavit. Types. In folio coriaceo ad Surinam, *Splitgerber 1205* (L, PC, isotypes).

Crossomitrium cruegeri Müll. Hal., Linnaea 38: 611. 1874. Protologue. Insulae Antillarum, Trinidad, monte Tamanaco: *Crüger* 9 Majo 1847 in ramis tenuibns [sic] appressam legit. Types. Trinidad, monte Tamanaco, *Crueger* (BM, NY, isotypes).

Crossomitrium spruceanum Müll. Hal., Linnaea 38: 613. 1874. Protologue. [Ecuador] Andes Quitenses, ad flumen Bombonasa, 1200 pedes altum: *Spruce Coll. No. 790*. Types. Andes Quitenses, fl. Bombonasa (1200 ped.), *Spruce, n. 790* (BM, F, FH, G, H, MICH, NY, S, US, isotypes).

Lepidopilum subepiphyllum Besch., Ann. Sci. Nat., Bot., sér. 6, 3: 228. 1876. *Crossomitrium subepiphyllum* (Besch.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 337. 1877. Protologue. Guadeloupe, sur les feuilles tombées à terre (*L'Herminier*; hb. Schimp.). Types. Guadeloupe, sur les feuilles tombées à terre, *L'Herminier* (BM, holotype; H, isotype).

Lepidopilum herminieri Schimp. *ex* Besch., Ann. Sci. Nat., Bot., sér. 6, 3: 228. 1876. *Crossomitrium herminieri* (Schimp. *ex* Besch.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 337. 1877. Protologue. Guadeloupe (*L'Herminier*; in herb. Schimp.). Types. Guadeloupe, *L.'Herminier* (BM, holotype; G, NY, isotypes).

Crossomitrium heterodontium Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32(1): 195. 1894. Protologue. [Costa Rica] Bois du Río Tuis, sur les feuilles des arbres. (*Pitt*[*ier*] *n° 5664*). Types. Bois du Río Tuis, *Tonduz* [*Pittier 5664*] (PC, holotype; NY, isotype).

Crossomitrium radulaeforme Müll. Hal., Malpighia 10: 514. 1896. Protologue. [Guyana] Guianae Anglicae, prope Georgetown ad cataractas "Marshall falls" fluvii Mazaruni a Cl. *J. Quelch*. Types. Prope Georgetown ad cataractas (Marshall Falls) fluvii Mazaruni, *Quelch 1274* (BM, NY, isotypes).

Crossomitrium ramulicola Müll. Hal., Malpighia 10: 514. 1896. Protologue. [Guyana] Guianae Anglicae, prope Georgetown ad cataractas "Marshall falls" fluvii Mazaruni a Cl. *J. Quelch*. Types. Prope Georgetown ad cataractas (Marshall Falls) fluvii Mazaruni, *Quelch 1276* (BM, FH, NY, isotypes).

Crossomitrium jamaicense Müll. Hal., Hedwigia 37: 245. 1898. Protologue. Jamaica, in montis humidis: *O. Hansen* 1897 in hb. Berolinensi. Type. Jamaica, *Hansen* (FH, isotype).

Crossomitrium sintenisii Müll. Hal., Flora 37: 244. 1898. Protologue. Portorico, Sierra de Luquillo, regione media montis Hymene, Junio 1885: *P. Sintenis* in Hb. Krug et Urban. Types. Sierra de Luquillo, regione media montis Hymene, Junio 1885: *P. Sintenis* in Hb. Krug et Urban (BM, FH, G, H, MICH, NY, PC, S, isotypes).

Plants slender to medium-sized, 2–5(–8) cm long, glossy, yellowish green. Stems prostrate, irregularly pinnately branched, reddish brown, usually complanate-foliate; cross section of stems with epidermis of 1–2 rows of small, thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2(–3) cells long, basal cell short-rectangular, reddish brown, upper cell(s) oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions and from contiguous basal leaf cells, smooth, reddish brown, unbranched

below with short branches at point of contact with substrate. Leaves in four rows, dimorphic. Lateral leaves erect at base and arching toward the substrate when dry, not or just barely overlapping with leaf above, oblong-subovate to lanceolate-oblong, 0.8–2.0 mm long, with nearly parallel sides, widest below the middle, short-acuminate or acute, carinate above. Dorsal leaves shorter and broader, ovate, erect-spreading when dry; margins uni- or biserrate above by projecting, frequently recurved, cell end walls, weakly serrate or entire at base, marginal cells often with 1 or more papillae, plane or narrowly recurved at the middle; costa none; upper and median cells linear to vermicular, 50–160 × 5–10 µm, firm-walled; basal cells near insertions 30–60 × 12–35 µm; alar cells undifferentiated. Asexual reproduction by brood bodies borne abaxial to the ventral leaf insertions or brood bodies borne on specialized branches tightly adherent to the substrate; brood leaves closely imbricate, orbicular, apiculate, cordate at base; brood bodies uniseriate, multicellular, 2 or more from a uniseriate, multicellular stalk, in clusters from initials at the ventral leaf bases. Dioicous. Perigonia and perichaetia sessile along stems and branches. Setae elongate, 4–12 mm long, red to red brown, scabrose to papillose above, smooth below, occasionally smooth throughout. Capsules inclined to suberect, ovoid to elliptic, neck weakly to moderately developed, 0.5–1.5 mm long; exothecial cells short-rectangular, variously collenchymatous; stomata on neck; opercula conic-rostrate, 0.5–1.5 mm long; annuli rudimentary; peristome diplolepideous; exostome teeth yellowish white, recurved when wet, incurved when dry (hydrocastique), narrowly triangular, both surfaces papillose throughout, dorsal trabeculae and median lines weak, ventral trabeculae moderately developed; endostome yellowish white, papillose, basal membranes high, segments linear, keeled, usually perforate, cilia absent. Spores 10–20 µm, lightly papillose. Calyptrae mitrate, reddish brown, smooth or roughened above and fimbriate at base, 1.0–1.5 mm long.

Illustrations. Hampe (1844, Pl. 1 1–10); Brotherus (1907a, Fig. 697 A–E); Brotherus (1925, Fig. 610 A–E); Bartram (1949, Fig. 142 A–D); Welch (1966, Figs. 47–65); Welch (1969, Figs. 39–45); Welch (1972a, Figs. 26–36); Florschütz-de Waard (1986, Fig. 112 a–e); Allen (1990, Figs. 7–14, 18, 20–21); Sharp *et al.* (1994, Fig. 620); Churchill and Linares (1995, Fig. 37 h–j); Duarte Bello (1997, Pl. 225); Buck (1998, Pl. 17 7–15); Gradstein *et al.* (2001, Fig. 165 A–C); Buck (2003, Fig. 88 G–O); Vaz and Costa (2006a, Figs. 60–66). Figure 163.

Habitat. On leaves or twigs, occasionally on vines, branches, and tree trunks, rarely on rotting logs or boulders; sea level to 2000 m.

Distribution in Central America. BELIZE. Cayo: *Allen 18269* (BRH, MO); Stann Creek: *Gentle 3498c* (MICH); Toledo: *Allen 18658* (MO). GUATEMALA. Alta Verapaz: *Türckheim 6905* (H, NY); Izabal: *Standley 72881* (CANM, FH, MICH); Petén: *Lundell 2707* (FH). HONDURAS. Atlántida: *Allen 17655* (MO, TEFH); Olancho: *Allen 12789* (MO); Yoro: *Allen 13569* (MO). NICARAGUA. Zelaya: *Stevens 4895A* (HNMN, MO). COSTA RICA. Alajuela: *Crosby 9996* (MO); Cartago: *Crosby 3647a* (CR, MO); Guanacaste: *Bowers 396a* (MO); Heredia: *Bowers CR-1667* (MO); Limón: *Crosby 3686* (MO); Puntarenas: *Dauphin 1443* (MO), Cocos Island: *Weber B-14268* (C, CANM, FH, H, MICH, MO, NY, UPS, US). PANAMA. Bocas del Toro: *Allen 5146B* (MO); Canal Area: *Tyson 1163C* (MO); Chiriquí: *Cornman 3038* (FH); Colón: *Crosby 10767* (MO, PMA); Darién: *Allen 8798* (MO); Panamá: *Crosby 10420* (MO, PMA); Veraguas: *Crosby 10163* (MO).

World range: Central America; Caribbean; Western and Northern South America.

Crossomitrium patrisiae is the most commonly occurring species of *Crossomitrium* in Central America. It is principally a tropical lowland species and mostly grows on leaves or twigs. *Crossomitrium patrisiae* often has brood branches at the stem and branch tips. The brood leaves are oval, orientated perpendicular to the substrate, and imbricate-overlapping. When well developed, the brood branches consist of three layers: a dense lower layer of rhizoids, a middle layer of brood bodies that originate from initials on the stem abaxial to the leaf insertions, and the brood leaves. The brood body initials have the same form and position as rhizoidal initials.

In its typical expression, *C. patrisiae* is a medium-sized plant with well-spaced leaves that do not or hardly overlap. The lateral leaves are lanceolate-oblong, with nearly parallel sides and a carinate, acuminate apex. When dry the lateral and dorsal leaves are stiffly erect at base but curved strongly above, causing the leaves to arch downward toward the substrate. This expression of the species is especially common in South America and is likely to be confused with *C. scabrisetum* or *C. acumina-*

tum, which are similar to *C. patrisiae* in habit, leaf shape, and brood branch form. *Crossomitrium scabrisetum*, moreover, is gametophytically identical to *C. patrisiae*, and differs only in having setae scabrose throughout. *Crossomitrium acuminatum* differs from *C. patrisiae* in having tightly recurved leaf margins with stout, strongly recurved dentations.

In Central America and the Caribbean, the common expression of *C. patrisiae* is a larger plant than the South American expression, with longer, broader leaves that are somewhat flattened rather than strongly arching when dry. Furthermore, the lateral leaves in this expression are closer together and often somewhat overlap. This expression generally does not produce brood branches. Instead, brood branches occur in dense clusters on the stems abaxial to the ventral leaf insertions. This expression of *C. patrisiae* has been called *C. jamaicense* or *C. sintenisii* in the Caribbean, and *C. cruegeri* or *C. ramulicola* in northern South America.

Crossomitrium epiphyllum and *C. patrisiae* are often found in mixed collections. Plants of *C. epiphyllum* grow strongly flattened to the substrate, and this aspect sharply contrasts with the erect-curved aspect of *C. patrisiae*. Furthermore, the ovate to oval leaves of *C. epiphyllum* are smaller than those of *C. patrisiae*, and it has erect brood branches with brood bodies borne on all sides.

4. *Crossomitrium rotundifolium* Herzog, Biblioth. Bot. 87: 134. 1916. Protologue. [Bolivia] Auf Gesträuchästen im feuchten Gebüsch bei San Miguelito, ca. 1400 m, [*Herzog*] *No. 2716*; an Ästchen in der Talschlucht bei Tablas, ca. 1800 m, [*Herzog*] *No. 4594*. Types (see Allen 1990). Bolivia, auf Gesträuch; Ästen im feuchten Gebüsch bei San Miguelito, *Herzog 2726* (JE, lectotype; H, S, isolectotypes). Bolivia, Ästchen in der Talschlucht bei Tablas, *Herzog 4594* (JE, syntype).

Crossomitrium splendens Broth., Rev. Bryol. 47: 38. 1921. Protologue. [Ecuador] *Prov. del Oriente.* Gualaquiza; in silva secus rivum "El Salado" [*Michel Allioni*]. Gualaquiza; ad truncum *Bixae orellanae* secus rivum Gualaquiza; 900 m [*Michel Allioni*]. Types (see Allen 1990). Ecuador, Prov. del Oriente, Gualaquiza, in silva secus rivum "El Salado," *Allioni 8404* (H, lectotype). Ecuador, Prov. del Oriente, Gualaquiza, ad truncum Bixae orellanae secus rivum Gualaquiza, *Allioni 525* (H, syntype).

Plants medium-sized to large, 4–6 cm long, glossy, yellowish green. Stems prostrate, irregularly pinnately branched, reddish brown, usually complanate-foliate; cross section of stems with epidermis of 1–2 rows of small, thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2(–3) cells long, basal cell short-rectangular, reddish brown, upper cell(s) oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions and from contiguous basal leaf cells, smooth, reddish brown, unbranched below, with short branches at point of contact with substrate. Leaves in four rows, dimorphic. Lateral leaves flattened to the substrate when dry, overlapping at base with leaf above, oblong-elliptic, 1.3–2.0 mm long, with convex sides widest above the middle, short-acuminate or acute, at times carinate above. Dorsal leaves shorter and broader, suborbicular to oblong, acute, flattened to the substrate when dry; margins uni- or biserrate above by projecting, cell end walls, weakly serrate or entire at base, marginal cells often with 1 or more papillae, plane; costa none; upper and median cells linear to vermicular, 70–150 × 7–10 µm, firm-walled; basal cells near insertions 50–125 × 17–25 µm; alar cells undifferentiated. Asexual reproduction by brood bodies borne abaxial to the ventral leaf insertions; brood bodies reddish brown, uniseriate, multicellular, 2 or more from a uniseriate, multicellular stalk, in clusters from initials at the ventral leaf bases. Dioicous (?). Sporophytes unknown.

Illustrations. Allen (1990, Figs. 41–44); Buck (2003, Fig. 89 & cover 4 photograph). Figure 164.

Habitat. On tree trunks, branches, and twigs, occasionally on leaves, rarely on rock; 20–1640 m.

Distribution in Central America. BELIZE. Toledo: *Whittemore 5501* (MO). GUATEMALA. Alta Verapaz: *Türckheim 6691* (H). NICARAGUA. Zelaya: *Stevens 4894* (MO). COSTA RICA. Cartago: *Crosby & Crosby 5916* (CR, MO); Heredia: *Bowers 797-a* (MO); Puntarenas: *Gómez 25370A* (MO); San José: *Alfaro 164* (FH, US). PANAMA. Bocas del Toro: *McDaniel 5080* (NY); Darién: *Allen 8923* (MO); Veraguas: *Crosby 10190* (MO).

World range: Central America; Western and Northern South America, Brazil.

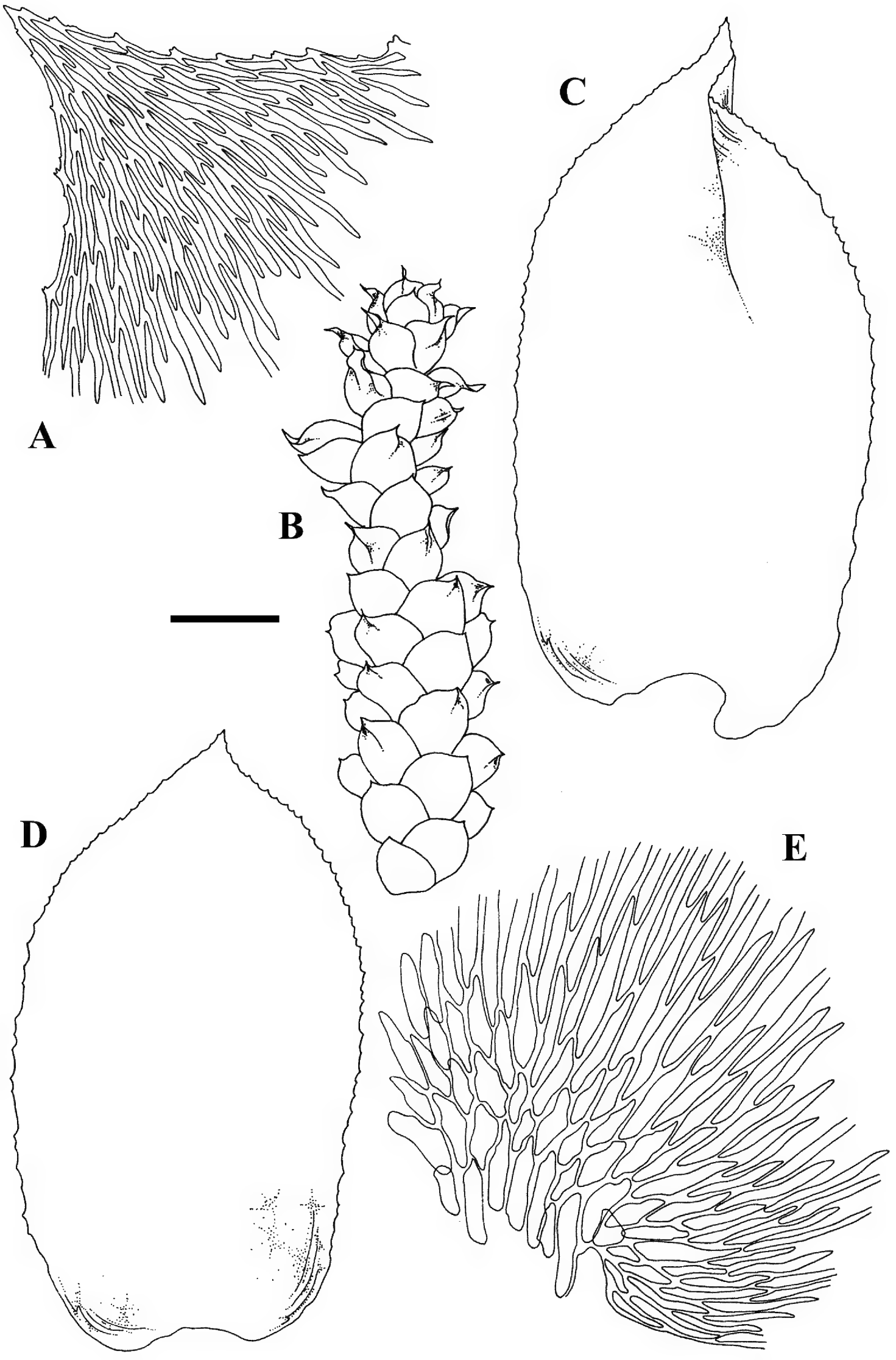


Figure 164. *Crossomitrium rotundifolium*. A. Leaf apex. B. Habit. C & D. Leaves. E. Basal and alar cells. Scale in mm: bar = 0.06 (A, E); bar = 0.28 (C, D); bar = 0.28 (B). B from *Crosby 14753*; all other figure parts from *Herzog 4594* (type).

Crossomitrium rotundifolium is a large species with plants that are flattened to the substrate. It has lateral leaves with convex sides that are broadest above the middle and overlap with the surrounding leaves. The leaf apices are often short and broad. The sporophytes of *C. rotundifolium* are unknown and it lacks specialized brood branches. It reproduces asexually by means of brood bodies that arise in dense clusters from initials on the basal, abaxial side of the ventral leaves. Stems with brood bodies are frequently twisted 180 degrees, thus exposing the brood bodies.

Crossomitrium rotundifolium is a mostly South American species, and it could be confused with *C. epiphyllum*, especially in regards to its flattened appearance and broad leaves. *Crossomitrium epiphyllum*, however, has smaller leaves (0.5–1.2 mm vs. 1.3–2.0 mm long) and specialized, erect brood branches. In Central America *C. rotundifolium* is very similar to the *jamaicense*- or *sintensii*-expressions of *C. patrisiae*. These expressions of *C. patrisiae* have broad lateral leaves that often overlap at base, and they tend to be flattened rather than arched when dry. They can be separated from *C. rotundifolium* by the presence of at least some lateral leaves that have parallel sides. Nevertheless, the separation of many collections remains problematic. Allen (1990) considered *C. sintensii* and *C. rotundifolium* synonyms, but treated *C. jamaicense* as a synonym of *C. patrisiae* even though admitting *C. sintensii* and *C. jamaicense* were sometimes inseparable in Hispaniola. Buck (2003) treated *C. sintensii* and *C. jamaicense* as synonyms of *C. patrisiae*, and restricted *C. rotundifolium* to South America. As noted by Allen (1990), the collection number given in the protologue of *C. rotundifolium* appears to be a typographical error.

5. *Crossomitrium saprophilum* Broth., Rev. Bryol. 47: 38. 1921. Protologue. [Ecuador] *Prov. del Oriente.* Gualaquiza; ad truncos putrescentes in silva montis Guayusa; 1000 m [*Michel Allioni*]. Type. Ecuador, Prov. del Oriente, Gualaquiza ad truncos putrescentes in silva montis Guayusa, *Allioni 611* (H, holotype).

Plants small, 1–3 cm long, glossy, yellowish green. Stems prostrate, irregularly pinnately branched, reddish brown, usually complanate-foliate; cross section of stems with epidermis of 1–2 rows of small, thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2 cells long, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions and from contiguous basal leaf cells, smooth, reddish brown, unbranched below, with short branches at point of contact with substrate. Leaves in four rows, dimorphic. Lateral leaves tightly flattened to the substrate and overlapping with leaf above, obovate, oval, or orbicular, 0.5–1.0 mm long, with convex sides widest above the middle, acute to shortly apiculate; dorsal leaves shorter and broader, orbicular, flattened to the stems when dry; margins weakly doubly serrate by projecting cell end walls at base, marginal cells often with 1 or more papillae, plane; costa none; upper and median cells linear to vermicular, 50–125 × 5–8 µm, firm-walled; basal cells near insertions 40–75 × 10–13 µm; alar cells undifferentiated. Asexual reproduction by brood bodies borne in dense terminal clusters on specialized, erect branches; brood leaves erect-appressed, shorter than vegetative leaves, orbicular, those at the apex forming a cup-like structure; brood bodies uniseriate, multicellular, 2 or more from a uniseriate, multicellular stalk. Dioicous (?). Sporophytes unknown.

Illustrations. Allen (1990, Figs. 33 & 35). Figure 165.

Habitat. On leaves, twigs, tree trunks, and rotting logs; 80–1100 m.

Distribution in Central America. BELIZE. Toledo: *Whittemore 5565A* (MO). GUATEMALA. Sololá: *Morton 4074 p.p.* (JE, S). COSTA RICA. Cartago: *Holm & Iltis* (MO); Limón: *Gutiérrez* (FH, US). PANAMA. Coclé: *Hunter & Allen 432A* (MO).

World range: Central America; Caribbean; Western South America, Brazil.

Crossomitrium saprophilum is a small plant, with strongly flattened, orbicular to obovate leaves. It is gametophytically identical to some expressions of *C. epiphyllum*, and has a broad, but scattered range that completely overlaps with that of *C. epiphyllum*. The two species differ only in features of their specialized brood branches. In *C. saprophilum*, the brood branch leaves are erect-appressed and the uppermost leaves form a loose cup that surrounds a dense, terminal cluster of propagula. In *C. epi-*

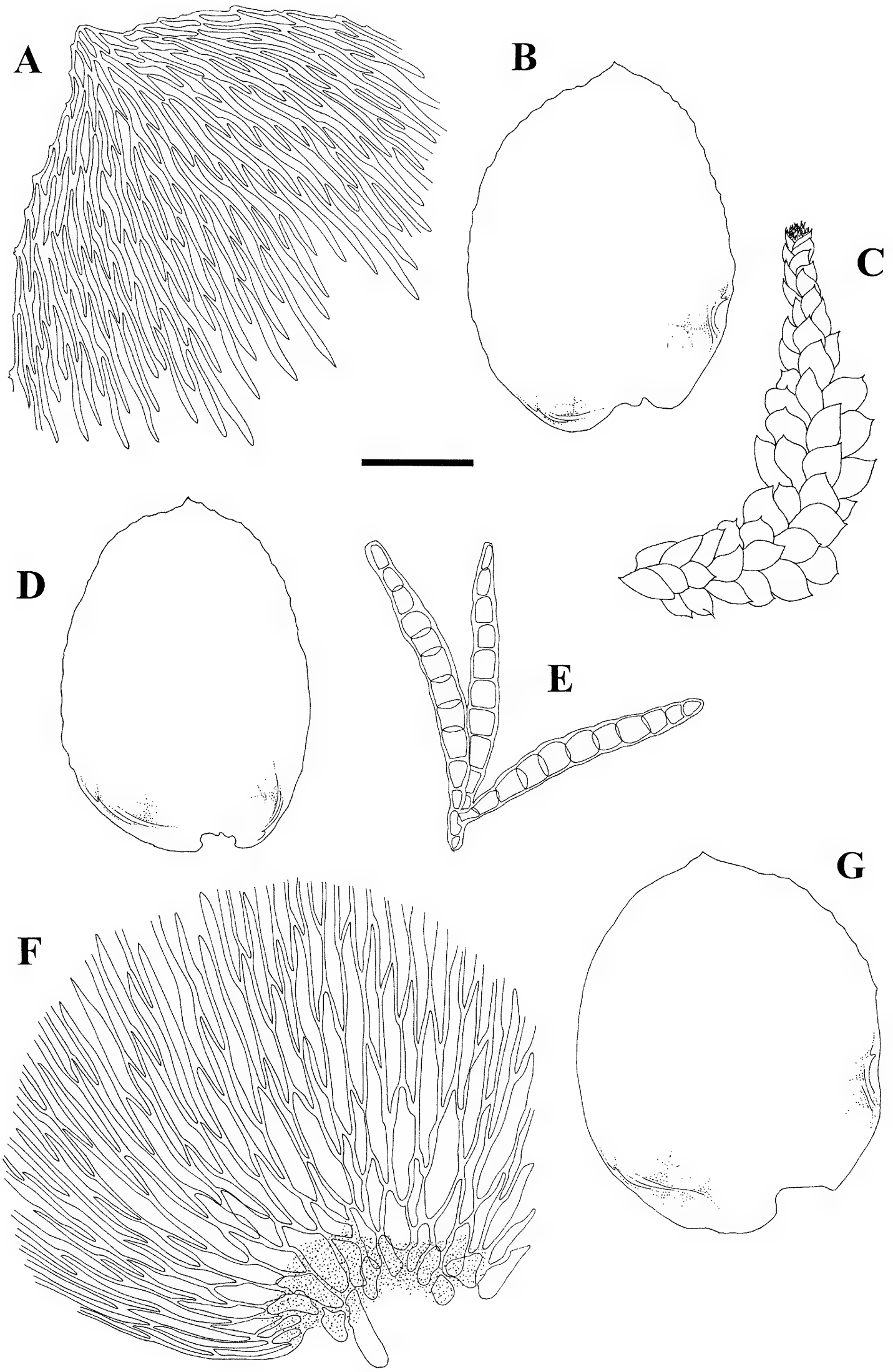
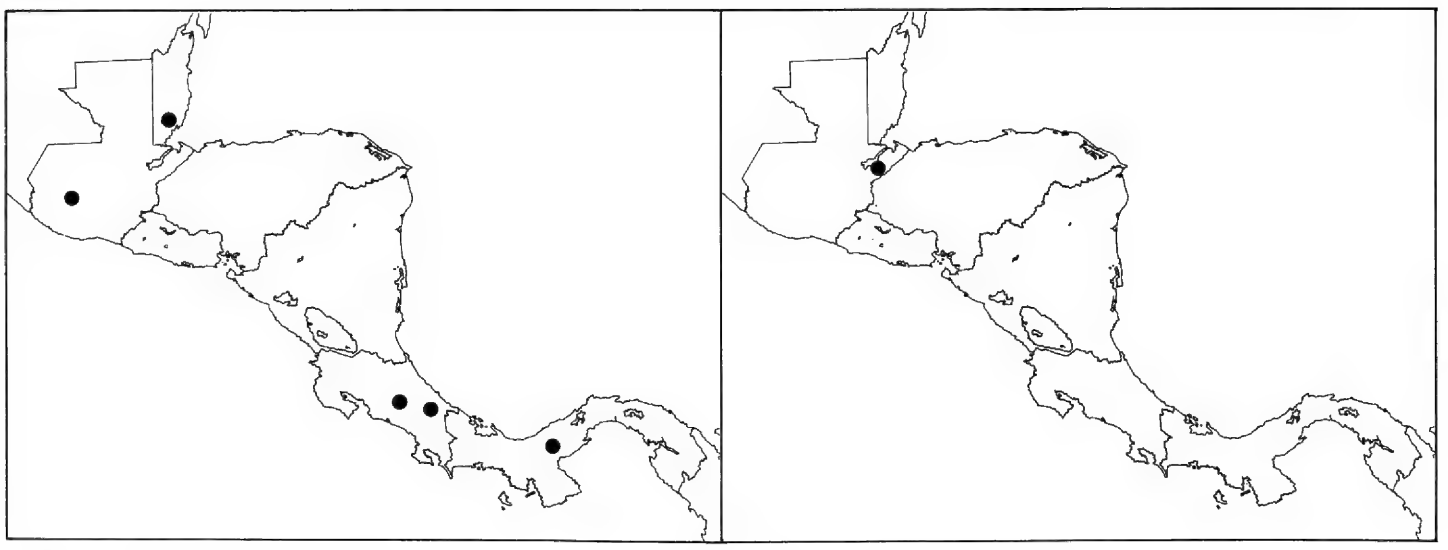


Figure 165. *Crossomitrium saprophilum*. A. Leaf apex. B, D & G. Leaves. C. Habit. E. Gemmae. F. Basal and alar cells. Scale in mm: bar = 0.06 (A, F); bar = 0.13 (E); bar = 0.28 (B, D, G); bar = 1.56 (C). C from *Whittemore 5565A*; all other figure parts from *Allioni 611* (type).



Crossomitrium saprophilum *Crossomitrium scabrisetum*

phyllum, the leaves of the brood branches are erect to erect-spreading and the propagula are borne along all sides of the brood branches abaxial to the leaves.

6. *Crossomitrium scabrisetum* E. B. Bartram, Bryologist 49: 119. 1946. Protologue. Guatemala. Dept. Izabal: damp forested slopes and barrancas, alt. 300–900 m, *Steyermark 41879*. Types. Guatemala. Dept. Izabal: damp forested slopes and barrancas, *Steyermark 41879* (FH, holotype; F, MICH, S, isotypes).

Plants slender, 2–3 cm long, glossy, yellowish green. Stems prostrate, irregularly pinnately branched, reddish brown, usually complanate-foliate; cross section of stems with epidermis of 1–2 rows of small, thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2(–3) cells long, basal cell short-rectangular, reddish brown, upper cell(s) oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions and from contiguous basal leaf cells, smooth, reddish brown, unbranched below, with short branches at point of contact with substrate. Leaves in four rows, dimorphic. Lateral leaves erect at base and arching toward the substrate when dry, not or just barely overlapping with leaf above, oblong-subovate to lanceolate-oblong, 1.4–1.7 mm long, with nearly parallel sides, widest below the middle, short-acuminate or acute, carinate above. Dorsal leaves shorter and broader, ovate, erect-spreading when dry; margins uni- or biserrate above by projecting, frequently recurved, cell end walls, weakly serrate or entire at base, marginal cells often with 1 or more papillae, plane or narrowly recurved at the middle; costa none; upper and median cells linear to vermicular, 60–125 × 7–10 µm, firm-walled; basal cells near insertions 50–90 × 15 µm; alar cells undifferentiated. Asexual reproduction by brood bodies borne abaxial to the ventral leaf insertions or borne on specialized branches tightly adherent to the substrate; brood leaves closely imbricate, orbicular, apiculate, cordate at base; brood bodies uniseriate, multicellular, 2 or more from a uniseriate, multicellular stalk, in clusters from initials at the ventral leaf bases. Dioicous. Perigonia and perichaetia sessile along stems and branches. Setae elongate, 5 mm long, red to red brown, densely tuberculose above, papillose below. Capsules inclined to suberect, ovoid to elliptic, tuberculate at base, 0.5–1.0 mm long; exothecial cells short-rectangular, moderately collenchymatous; stomata on neck; opercula conic-rostrate, 0.4–0.5 mm long; annuli rudimentary; peristome diplolepideous; exostome teeth yellowish white, recurved when wet, incurved when dry (hydrocastique), narrowly triangular, both surfaces papillose throughout, dorsal trabeculae and median lines weak, ventral trabeculae moderately developed; endostome yellowish white, papillose, basal membranes low, segments linear, keeled, entire or perforate, cilia absent. Spores 12–15 µm, lightly papillose. Calyptrae mitrate, reddish brown, roughened above and fimbriate at base, 1.0 mm long.

Illustrations. Bartram (1949, Fig. 142 E–H); Welch (1974, Figs. 86–100); Allen (1990, Figs. 1, 5, 15–17, 18). Figure 166.

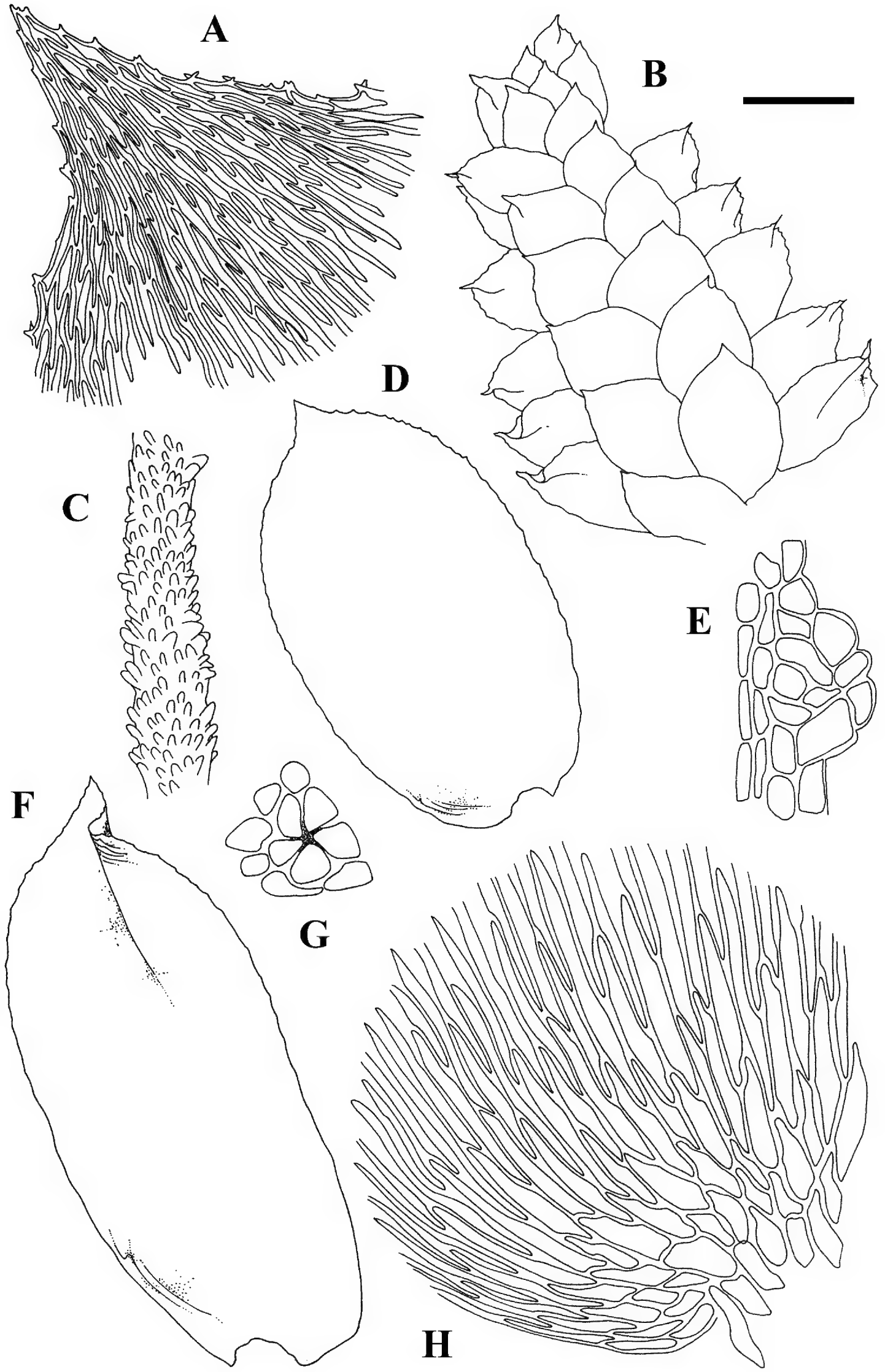


Figure 166. *Crossomitrium scabrisetum*. A. Leaf apex. B. Habit. C. Seta. D. Dorsal leaf. E. Capsule struma. F. Lateral leaf. G. Stoma. H. Basal and alar cells. Scale in mm: bar = 0.06 (A, E, G, H); bar = 0.18 (C); bar = 0.28 (D, F); bar = 0.6 (B). All figure parts from *Steyermark 41879* (type).

Habitat. Epiphyllous; 300–900 m.
Distribution in Central America. GUATEMALA. Izabal: *Steyermark 41879* (F, FH, MICH, S).
World range: Central America.

Crossomitrium scabrisetum is known only from the type collection. The plants have crowded leaves that are flattened at the branch and stem tips, giving them a distinctive appearance. However, some expressions of the gametophytically variable *C. patrisiae* are nearly identical to *C. scabrisetum*; often the two cannot be distinguished when sporophytes are absent. It is possible that many sterile collections named *C. patrisiae* from Central America may actually be *C. scabrisetum*. *Crossomitrium patrisiae* differs from *C. scabrisetum* in having setae that are scabrose to papillose above but smooth below or smooth throughout, and non-tuberculose capsule necks. Bartram (1946) emphasized the short setae of *C. scabrisetum* as another way to distinguish it from *C. patrisiae*, but the setae of *C. patrisiae* are sometimes as short as those of *C. scabrisetum*.

6. *Cyclodictyon* Mitt., J. Linn. Soc., Bot. 7: 163. 1864. *Hookeria* Sm. sect. *Cyclodictyon* (Mitt.) Mitt., J. Linn. Soc., Bot. 12: 340. 1869.

Plants small to medium-sized, pale greenish, green, yellowish green, or red, in thin or dense mats. Stems prostrate, irregularly branched, hyaline to yellowish when young, becoming reddish with age, often complanate-foliate; stems in cross section with a 1-stratose hyalodermis, subepidermis of 1–2 rows of smaller, thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia foliose; axillary hairs 2 cells long, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves variously contorted, sometimes undulate when dry, variously dimorphic (lateral leaves and ventral/dorsal), asymmetric or symmetric, concave, ovate, oblong-ovate, oblong, or oblong-lanceolate, apiculate, mucronate, cuspidate or abruptly slenderly long-acuminate to hair-pointed; margins serrate, serrulate, subentire or entire, often broadly inflexed below on one side, bordered by 1–7 rows of narrow, elongate cells confluent in the apex; costae double, ending 2/3–7/8 the leaf length, diverging throughout, one branch sometimes reaching to and more or less fusing with the border, at times projecting at the apices, sometimes with swollen teeth on upper dorsal surface; cells smooth, upper cells broadly hexagonal, rounded-hexagonal or oval-hexagonal, laxly bulging, median and lower cells oblong-rectangular to long-rectangular; alar cells undifferentiated. Asexual reproduction occasionally by light green to brownish filaments at the base of the dorsal surface of the costae and abaxial to the leaf insertions. Autoicous or dioicous. Perigonia and perichaetia sessile along stems and branches. Setae elongate, red to red brown, smooth. Capsules inclined to pendent, short-cylindric, neck moderately developed; exothecial cells reddish, quadrate to shortly oblate at mouth, those below yellowish, short-rectangular, with thick vertical walls and thin horizontal walls, variously collenchymatous; stomata 2–4-celled, rudimentary, on neck; opercula long-rostrate, conic at base; annuli rudimentary, deciduous; peristome diplolepideous; exostome teeth narrowly triangular, with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface dark red, densely and closely striate below, coarsely papillose above, primary walls yellow, smooth, ventral surface hyaline to yellowish, deposition thin, lightly papillose, median lines weak; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not or faintly perforate, cilia absent. Calyptrae mitrate, yellowish white, irregularly lobed at base, naked, smooth.

Cyclodictyon is a genus of 90 species (Crosby *et al.* 2000) found throughout the tropics and subtropics. The genus often grows prostrate in wet places, and as a result its lateral leaves are usually distinctly different from the ventral and dorsal leaves. The stems of *Cyclodictyon* have a well-developed hyalodermis. Its leaves are variously bordered by 1–7 rows of elongate, narrow cells, and they have very large, smooth, thin-walled, bulging leaf cells and long, usually slender, double costae. The genus is typically thought to have more or less isodiametric upper leaf cells, but leaf cell form is extremely variable within the genus, and single leaves can have a mixture of isodiametric cells and cells that are longer than wide. Although the costae in the genus are usually slender and weak, there are some species in which the costae bulbously project at the tips and have swollen teeth on the upper dorsal sur-

face. The sporophytes of Central American *Cyclodictyon* species are remarkably uniform: setae long, red, smooth; capsules inclined, short-cylindric; lower exothecial cells weakly collenchymatous (thick vertical walls and thin horizontal walls); stomata rudimentary, two- to four-celled; opercula long-rostrate; exostome teeth broadly furrowed, closely striate below; endostome basal membranes high, segments broad, cilia absent; calyptrae mitrate, naked, irregularly lobed at base.

The combination of bordered leaves with long, slender costae and enlarged, bulging, commonly isodiametric cells makes *Cyclodictyon* fairly easy to recognize. The genus appears close to *Thamniopsis*, *Amblytropis*, and *Lepidopilum*. Some species of *Thamniopsis* have a leaf cell areolation nearly identical to that of *Cyclodictyon*, but all members of the genus differ from *Cyclodictyon* in lacking a leaf border. *Lepidopilum* and *Amblytropis* are the only other Central American members of the Hookeriaceae in which there are species that have bordered leaves. *Amblytropis* is gametophytically nearly identical to *Cyclodictyon*. It differs only in having setose setae and exostome teeth that are papillose throughout. *Lepidopilum* differs from *Cyclodictyon* in often having asexual propagula in the leaf axils, leaf cells that are usually long-hexagonal, shorter costae that often end at or below midleaf, typically papillose or scabrous setae, exostome teeth that are papillose throughout, and often hairy calyptrae.

The name *Cyclodictyon* combines the Greek *cyclos* (circle) and *dictyon* (net); it refers to the upper leaf cells of the genus that are often enlarged and rounded-hexagonal, forming a net-like pattern.

1. Leaves bordered by 4–7 rows of elongate cells . . . . . 7. *C. subtortifolium*
1. Leaves bordered by 1–3 rows of elongate cells 2

2. Leaf border obsolete, 1 cell wide . . . . . 9. *C. varians*
2. Leaf border distinct, 1–3 cells wide, never entirely of 1 row of cells 3

3. Upper leaf margins entire to subentire 4
3. Upper leaf margins serrate or serrulate, rarely subentire 8

4. Plants small, 0.3–0.6 cm high; leaves 0.8–1.0 mm long, with clusters of green, septate gemmae borne on reddish brown filaments at base of costae and stem abaxial to the leaf insertion . . . . . 3. *C. crosbyi*
4. Plants larger, 1–10 cm high; leaves 1–4 mm long, asexual gemmae absent 5

5. Plants 5–10 cm high; leaves 3.5–4.0 mm long, strongly undulate when wet or dry . . . . . 8. *C. validirugosum*
5. Plants 1–4 cm high; leaves 1.0–2.2 mm long, not undulate or only with margins undulate 6

6. Leaves apiculate to cuspidate; upper leaf cells 30–60 µm wide . . . . . 4. *C. fendleri*
6. Leaves slenderly acuminate or hair-pointed; upper leaf cells 18–32 µm wide 7

7. Plants often red to reddish tinged, at times yellowish green; leaf margins undulate when dry; upper leaf cells mostly longer than wide . . . . . 6. *C. rubrisetum*
7. Plants green to yellowish, rarely reddish tinged; leaf margins plane when dry; upper leaf cells mostly isodiametric . . . . . 5. *C. roridum*

8. Leaves slenderly acuminate or hair-pointed; upper leaf cells 18–32 µm wide 9
8. Leaves apiculate to cuspidate; upper leaf cells 30–60 µm wide 10

9. Plants often red to reddish tinged, at times yellowish green; leaf margins undulate when dry; upper leaf cells mostly longer than wide . . . . . 6. *C. rubrisetum*
9. Plants green to yellowish, rarely reddish tinged; leaf margins plane when dry; upper leaf cells mostly isodiametric . . . . . 5. *C. roridum*

10. Leaf cusp filled with elongate cells; leaf border 2–3 cells wide; costae usually projecting as blunt knob and toothed on upper dorsal surface . . . . . 1. *C. albicans*
10. Leaf apiculus filled with short cells; leaf border 1–2 cells wide; costae rarely projecting as a blunt spine, entire on dorsal surface . . . . . 2. *C. bicolor*

1. *Cyclodictyon albicans* (Hedw.) Kuntze, Revis. Gen. Pl. 2: 835. 1891. *Leskea albicans* Hedw., Sp. Musc. Frond. 218. 1801. *Pterygophyllum albicans* (Hedw.) Brid., Muscol. Recent. Suppl. 4: 150. 1819. *Hookeria albicans* (Hedw.) Hook. & Grev., Edinburgh J. Sci. 2: 230. 1825. Protologue. Jamaica [*Swartz*].

Hookeria lindigiana Hampe, Linnaea 32: 156. 1863. *Cyclodictyon lindigianum* (Hampe) Kuntze, Revis. Gen. Pl. 2: 835. 1891. Protologue. [Colombia] In sylv. Tequendama Canoas et Cipacon ad truncos arbor., 2500–2600 metr., Junio–Aug. [*Lindig*] *no. 2091*.

Hookeria nicaraguensis Broth. *in* H. A. Crum, Bryologist 55: 163. 1952, invalid name, lacks a description and cited in synonymy. Based on: Nicaragua. Volcán Mombacho, Dept. Granada, *C. F. Baker 2503* (FH, MO, NY, US).

Plants small to medium-sized, 10–30 mm long, pale greenish, green, yellowish green, occasionally reddish tinged, in thin or dense mats. Stems prostrate, irregularly branched, hyaline to yellowish when young, becoming reddish with age, somewhat complanate-foliate; stems in cross section with 1-stratose hyalodermis, subepidermis of 1–2 rows of smaller, thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia foliose; axillary hairs fugacious, 2 cells long, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves weakly contorted when dry. Lateral leaves erect-spreading when dry, wide-spreading when wet, asymmetric, ovate, oblong-ovate, or oblong, 1–2 mm long, abruptly acuminate, concave; margins sharply serrate to serrulate above, subentire below, broadly inflexed below on one side, distinctly bordered by 2–3 rows of narrow, elongate cells confluent in the apices; costae double, ending 3/4–7/8 the leaf length, diverging throughout, one branch often reaching to and more or less fusing with the border, projecting knob-like at the apices and often with swollen teeth on upper dorsal surface; cells smooth, apical cells elongate, upper cells broadly hexagonal, 30–60 µm long, laxly bulging, median and lower cells oblong-rectangular to long-rectangular; alar cells undifferentiated. Ventral and dorsal leaves symmetric, ovate, gradually acuminate; margins plane; costae slender, ending 2/3 the leaf length, not projecting at the tips. Asexual reproduction absent. Autoicous. Perigonia and perichaetia sessile along stems and branches. Setae elongate, 13–20 mm long, red to red brown, smooth. Capsules inclined to pendent, short-cylindric, neck moderately developed, 1.5–2.0 mm long; exothecial cells in 2–3 rows, reddish, quadrate to shortly oblate at mouth, those below yellowish, short-rectangular with thick vertical walls and thin horizontal walls, not or obscurely collenchymatous; stomata 2–4-celled, rudimentary, on neck; opercula long-rostrate, conic at base, 1.0–1.2 mm long; annuli rudimentary, deciduous; peristome diplolepideous; exostome teeth narrowly triangular, with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface dark red, densely and closely striate below, coarsely papillose above, primary walls yellow, smooth, ventral surface hyaline to yellowish, deposition thin, lightly papillose, median lines weak; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not or faintly perforate, cilia absent. Spores rounded to oval, 8–12 µm, faintly papillose. Calyptrae mitrate, yellowish white, irregularly lobed at base, naked, smooth, 1.5–2.0 mm long.

Illustrations. Bartram (1949, Fig. 133 D–F); Sharp *et al.* (1994, Fig. 585; Fig. 586, as *C. rubrisetum*); Churchill and Linares (1995, Fig. 38 a & b); Duarte Bello (1997, Pl. 237); Buck (1998, Pl. 10 1–5); Vaz and Costa (2006a, Figs. 67–73). Figure 167.

Habitat. On limestone, travertine, or rocks in or along streams, stream banks, roots, humus, soil, leaves, and rotting sticks or logs; 65–2600 m.

Distribution in Central America. BELIZE. Cayo: *Allen 18341* (BRH, MO); Toledo: *Allen 18553* (MO). GUATEMALA. Alta Verapaz: *Steyermark 45553* (F, FH); Izabal: *Steyermark 41899* (F, FH); Quetzaltenango: *Standley 85061* (F, NY); Quiché: *Sharp 2475* (MO, NY, US). EL SALVADOR. Santa Ana: *Watson 77* (MO). HONDURAS. Atlántida: *Allen 17447* (MO); Comayagua: *Allen 13695* (MO); Francisco Morazán: *Allen 12386* (MO, TEFH); Lempira: *Allen 11928* (MO); Ocotepeque: *Allen 14496* (MO); Olancho: *Allen 12421* (MO, TEFH); Santa Bárbara: *Allen 11688* (MO, TEFH). NICARAGUA. Granada: *Baker 2503* (FH, MO, NY, US); Jinotega: *Croat 43085* (MO); Matagalpa:

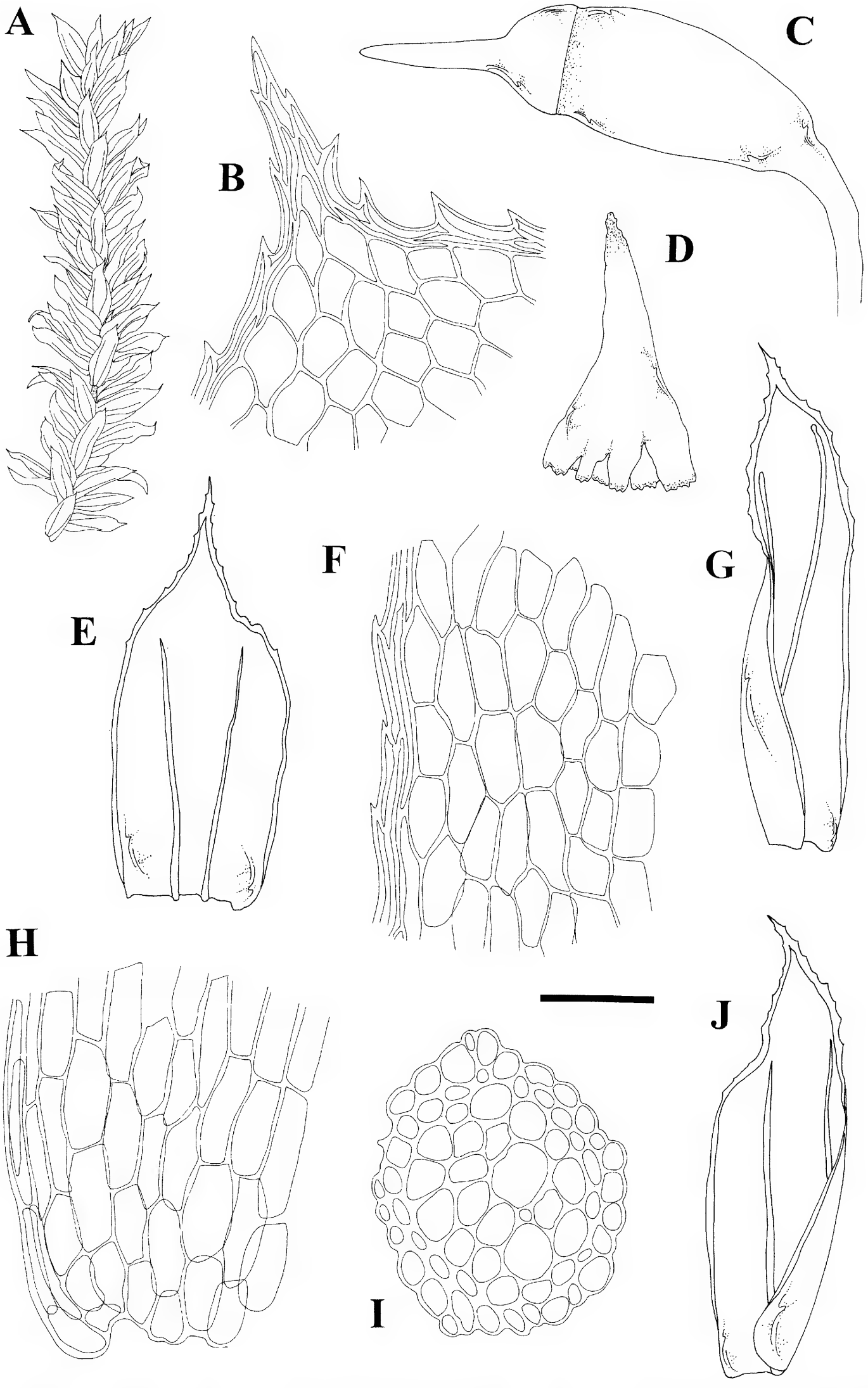
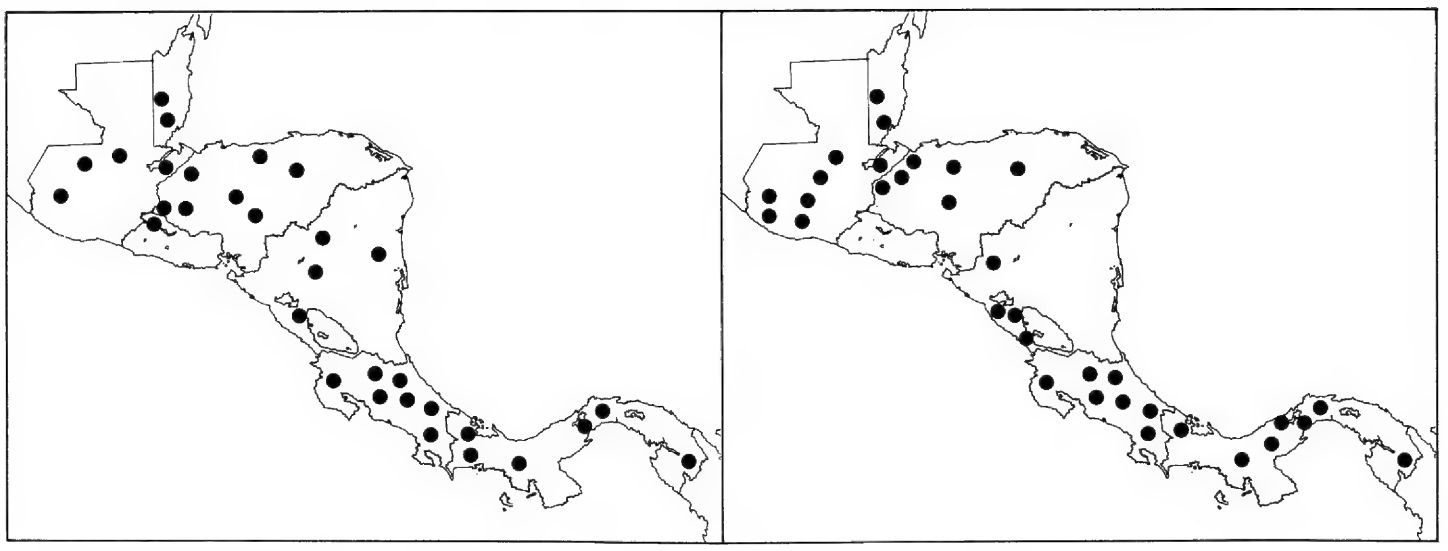


Figure 167. *Cyclodictyon albicans*. A. Habit. B. Leaf apex. C. Seta, capsule, and operculum. D. Calyptra. E. Ventral leaf. F. Median leaf cells and margin. G & J. Lateral leaves. H. Basal and alar cells. I. Stem in cross section. Scale in mm: bar = 0.08 (B, F, H, I); bar = 0.4 (E, G, J); bar = 0.71 (C, D); bar = 2.5 (A). C, D from *Watson ES-0007*; all other figure parts from *Allen 14496*.



Cyclodictyon albicans *Cyclodictyon bicolor*

Richards et al. 3762a (F); Zelaya: *Proctor et al. 27270* (MO, NY). COSTA RICA. Alajuela: *Crosby 10012* (MO); Cartago: *Liesner 14351* (MO); Heredia: *Nee 14366* (CR, MO); Guanacaste: *Standley & Valerio 45775* (FH, NY, US); Limón: *Gutierrez* (FH); Puntarenas: *Lyon 253* (CR, MO); San José: *Crosby & Crosby 6395* (MO). PANAMA. Bocas del Toro: *Allen 5251* (MO); Canal Area: *Willis* (F, FH); Chiriquí: *Croat 15902D* (MO); Darién: *Folsom 4336* (MO, NY, PMA); Panamá: *McDaniel 6890a* (MO); Veraguas: *Crosby 10248* (MO).

World range: Mexico; Central America; Caribbean; Western, Northern, and Southern South America, Brazil.

Cyclodictyon albicans is usually a medium-sized species, with a pale green color and slightly crisped leaves when dry. Its lateral leaves are typically oblong-ovate to oblong and asymmetric, with one margin broadly inflexed, while the dorsal and ventral leaves are ovate and symmetric, with plane margins. However, there is considerable intergradation between the two leaf types. Only the lateral leaves should be used to identify the species. The leaf margins are strongly bordered by 2–3 rows of cells that merge into a fairly long apex, and they are sharply serrate to serrulate. The leaf cells are enlarged and thin-walled, with the upper cells usually more or less hexagonal. However, leaf cell form is extremely variable in *C. albicans*; often single plants have some leaves with all upper leaf cells isodiametric, while other leaves have upper cells with a mixture of isodiametric cells and cells longer than wide. The double costae diverge throughout the leaf, and curiously one branch often merges with the leaf border. The costae end in large, projecting, bulbous cells, and there are often swollen teeth on the upper dorsal surface.

This species has been greatly misunderstood in Central America and is often confused with *C. bicolor*, *C. varians*, and *C. rubrisetum*. The first two species belong to the group of *Cyclodictyon* with enlarged, thin-walled, more or less hexagonal upper leaf cells. *Cyclodictyon bicolor* and *C. varians* differ from *C. albicans* in having much weaker leaf borders (*C. bicolor* border 1–2 cells wide, *C. varians* border more or less obsolete, never more than 1 cell wide) that are less strongly serrate. As a result of their weaker borders, the leaf apices in both species are filled by short rather than elongate cells. In addition, the costae in *C. bicolor* and *C. varians* rarely end in a projecting cell, and are never toothed on the dorsal surface. The confusion in Central America between *C. rubrisetum* and *C. albicans* is due to a misunderstanding of *C. rubrisetum* and a failure to appreciate the variability of upper leaf cell form in *C. albicans*. *Cyclodictyon rubrisetum* is a reddish plant, with smooth or subentire leaf margins and weak costae that are smooth on the dorsal surface and do not project at the tips. The upper leaf cells in *C. rubrisetum* are generally longer than wide, and this apparently has caused confusion with forms of *C. albicans* that also have upper cells longer than wide. *Cyclodictyon albicans* differs from *C. rubrisetum* in its pale green to green color, serrate to serrulate leaf margins, and costae that are usually toothed at back and end in projecting tips.

Cyclodictyon fendleri is another member of the large-celled *Cyclodictyon* group that has strongly bordered leaves identical to those of *C. albicans* in shape. In addition, its apiculus is usually filled

with elongate cells. It differs from *C. albicans* in having mostly entire (sometimes obscurely serrulate) leaf margins. In addition, the costae only occasionally end in weakly projecting cells, and they are rarely toothed on the dorsal surface.

2. *Cyclodictyon bicolor* (Schimp. *ex* Besch.) Kuntze, Revis. Gen. Pl. 2: 835. 1891. *Hookeria bicolor* Schimp. *ex* Besch., Ann. Sci. Nat., Bot. sér. 6, 3: 232. 1876. Protologue. Guadeloupe (*L'Herminier*, in herb. Schimp.).

Hookeria albicaulis Schimp. *ex* Besch., Ann. Sci. Nat., Bot. sér. 6, 3: 232. 1876. *Cyclodictyon albicaule* (Schimp. *ex* Besch.) Kuntze, Revis. Gen. Pl. 2: 835. 1891. Protologue. Guadeloupe (*L. Herminier*, *n*^{o} *5*, in herb. Mus. Par.; *Husnot*).

Hookeria prasiophylla Besch., J. Bot. (Morot) 8: 177. 1894. *Cyclodictyon prasiophyllum* (Besch.) Broth., Nat. Pflanzenfam. I(3): 935. 1907. Protologue. Guadeloupe: le Gommier, Sainte-Rose, 27 avril 1877 (*Ed. Marie, n*^{os} *118 et 699*).

Hookeria ulophylla Besch., J. Bot. (Morot) 8: 177. 1894. *Cyclodictyon ulophyllum* (Besch.) Broth., Nat. Pflanzenfam. I(3): 936. 1907. Protologue. Guadeloupe, sur la terre humide. (*Ed. Marie, n*^{o} *659*).

Hookeria antillarum Broth. *in* Urb., Symb. Antill. 3: 427. 1903, illegitimate homonym, not *Hookeria antillarum* Mitt., J. Linn. Soc., Bot. 12: 343. 1869. *Cyclodictyon dussii* Broth., Nat. Pflanzenfam. I(3): 935. 1907, new name for *H. antillarum* Broth. *in* Urb. Protologue. Hab. in Martinique ad viam inter Gros-Morne et les Deux Choux ad ligna putrida: *Duss n. 68* (in Herb. Berol.).

Hookeria densifolia Broth. *in* Urb., Symb. Antill. 3: 428. 1903. *Cyclodictyon densifolium* (Broth.) Broth., Nat. Pflanzenfam. I(3): 936. 1907. Protologue. Hab. in Martinique ad Macouba in rupibus: *Duss n. 274* (in Herb. Berol.), in Calebasse ad ligna putrida: *Duss n. 9* (in Herb. Berol.).

Hookeria limbatula Broth. *in* Urb., Symb. Antill. 3: 429. 1903. *Cyclodictyon limbatulum* (Broth.) Broth., Nat. Pflanzenfam. I(3): 936. 1907. Protologue. Hab. in Guadeloupe in Morne Gobelin ad truncos arborum: *Duss n. 237* (in Herb. Berol.).

Cyclodictyon humectatum Cardot, Rev. Bryol. 37: 50. 1910. Protologue. [Mexico] État de Morelos: près de Cuernavaca, rochers humides, 1907 et 1908 ([*Pringle*] *n*^{os} *10528, 15090*). Types. Plantae Mexicanae. Morelos, under wet cliffs of barranca near Cuernavaca, 4500 ft., 1 Aug., 1908. *C. G. Pringle 10528* (MO, lectotype, designated here; NY, US, isolectotypes), *syn. nov.*

Plants medium-sized, 10–30 mm long, pale greenish, green, yellowish green, occasionally reddish tinged, in thin or dense mats. Stems prostrate, irregularly branched, hyaline to yellowish when young, becoming reddish with age, complanate-foliate; stems in cross section with 1-stratose hyalodermis, subepidermis of 1–2 rows of smaller, thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia foliose; axillary hairs fugacious, 2–3 cells long, basal cell short-rectangular, reddish brown, upper cell(s) oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves weakly contorted when dry. Lateral leaves erect-spreading when dry, widespreading when wet, asymmetric, oblong-ovate or oblong, 1–2 mm long, gradually acute to mucronate, concave; margins bluntly serrate, occasionally sharply serrate above, subentire below, broadly inflexed below on one side, bordered by 1–2 rows of narrow, elongate cells confluent at the apices; costae double, ending 3/4–7/8 the leaf length, diverging throughout, occasionally projecting at the apices and rarely with swollen teeth on upper dorsal surface; cells smooth, upper cells broadly hexagonal, 30–50 µm long, laxly bulging, median and lower cells oblong-rectangular to long-rectangular; alar cells undifferentiated. Ventral and dorsal leaves symmetric, ovate, gradually acuminate; margins plane; costae slender, ending 2/3 the leaf length, not projecting at the tips. Asexual reproduction absent. Dioicous. Perigonia and perichaetia sessile along stems and branches. Setae elongate, 15–25 mm long, red to red brown, smooth. Capsules inclined to pendent, short-cylindric, neck moderately developed, 1–2 mm long; exothecial cells in 2–3 rows, reddish, quadrate to shortly oblate at mouth, those below short-rectangular, more or less collenchymatous; stomata 2–4-celled, rudimentary, on neck; opercula long-rostrate, conic at base, 1.0–1.2 mm long; annuli rudimentary, deciduous; peristome diplolepideous; exostome teeth narrowly triangular, with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface dark red, densely and closely striate below, coarsely papillose above, primary walls yellow, smooth, ventral surface hyaline to yellowish, deposition thin, lightly papillose, median lines weak; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not or faintly perforate, cilia absent. Spores rounded

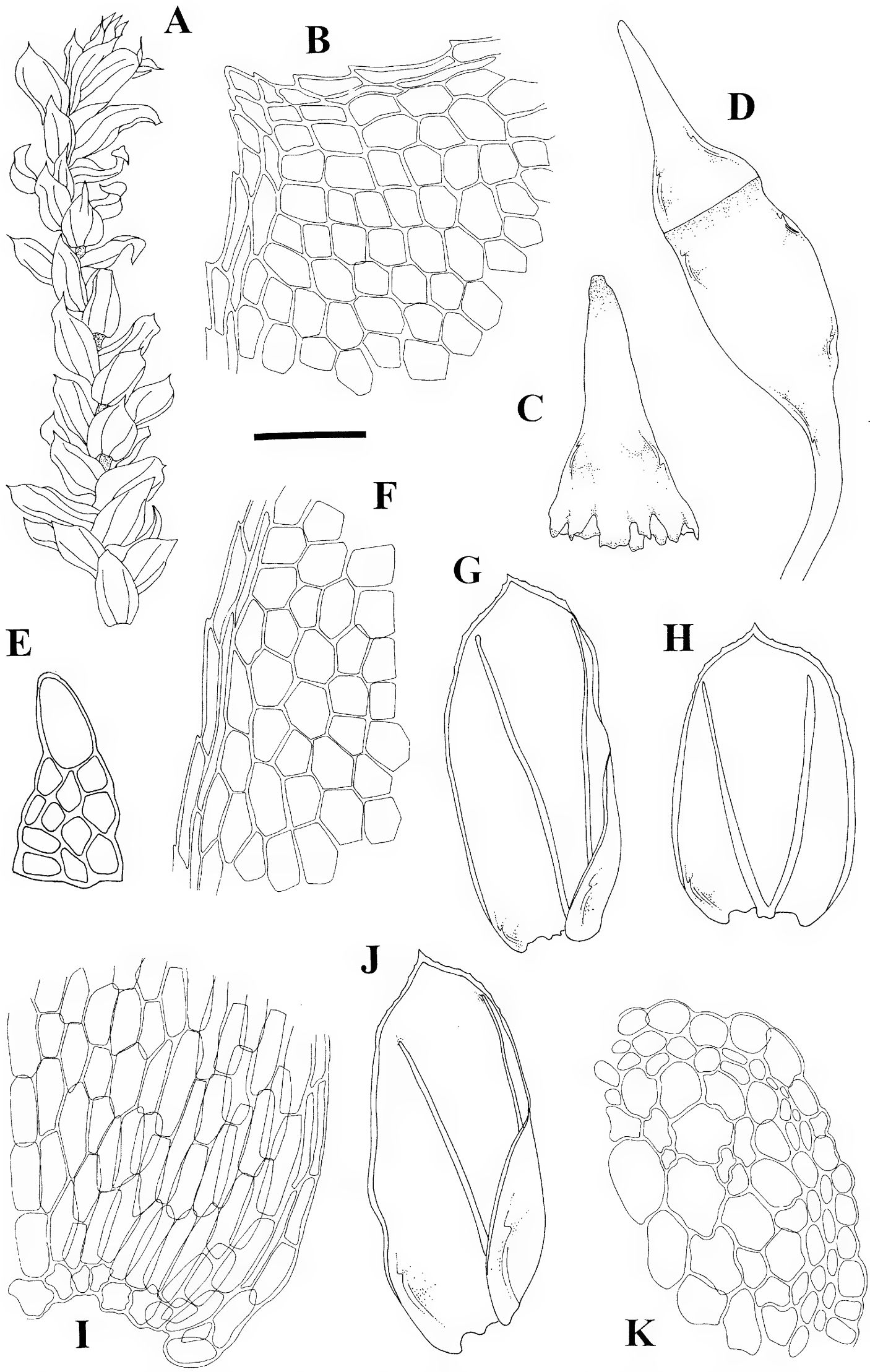


Figure 168. *Cyclodictyon bicolor*. A. Habit. B. Leaf apex. C. Calyptra. D. Seta, capsule, and operculum. E. Pseudoparaphyllia. F. Median leaf cells and margin. G & J. Lateral leaves. H. Dorsal leaf. I. Basal and alar cells. K. Stem in cross section. Scale in mm: bar = 0.04 (E); bar 0.08 (B, F, I, K); bar = 0.5 (G, H, J); bar = 0.71 (C, D); bar = 1.56 (A). C, D from *Allen 13606*; all other figure parts from *Allen 11621*.

to oval, 12–18 μm, smooth to faintly papillose. Calyptrae mitrate, yellowish white, irregularly lobed at base, naked, smooth, 1.5 mm long.

Illustrations. Sharp *et al.* (1994, Fig. 584); Buck (1998, Pl. 9 4–8). Figure 168.

Habitat. On rocks, boulders, travertine, or soil submerged in or along streams, and on trees, rotting logs, or stones in woods; 70–2250 m.

Distribution in Central America. BELIZE. Cayo: *Allen 18312* (BRH, MO); Toledo: *Allen 18582* (BRH, MO). GUATEMALA. Alta Verapaz: *Standley 70728* (F, FH); Baja Verapaz: *Sharp 2664* (FH, NY); Escuintla: *Standley 89531* (F, FH); Izabal: *Steyermark 41781* (F, FH); Quetzaltenango: *Kellerman* (US); Retalhuleu: *Standley 87194* (F, FH, NY); Sacatepéquez: *Standley 58987* (F, FH, NY). HONDURAS. Cortés: *Allen 14322* (MO); Comayagua: *Allen 11753* (MO, TEFH); Copán: *Allen 17738* (MO); Olancho: *Allen 12423* (MO, TEFH); Santa Bárbara: *Allen 11621* (MO, TEFH); Yoro: *Allen 13570* (MO). NICARAGUA. Estelí: *Granzow de la Cerda et al. CG-1567* (DUKE, MO); Managua: *Garnier 714* (FH, NY, US); Masaya: *Standley 8729* (F); Rivas: *Granzow de la Cerda GC-1651* (DUKE). COSTA RICA. Alajuela: *Lyon 623* (MO); Cartago: *Standley & Valerio 46988* (FH, NY, US); Guanacaste: *Alfaro* (FH, US); Heredia: *Crosby & Crosby 6020* (CR, MO); Limón: *Daly 125* (MO); Puntarenas: *Dauphin 1709* (MO); San José: *Stiles & Martin 5* (US). PANAMA. Bocas del Toro: *Allen 5521* (MO); Canal Area: *Crosby 10798* (MO, PMA); Coclé: *Meeker* (F, FH, MO, NY); Colón: *Crosby 10448* (MO, PMA); Darién: *Allen 8654* (MO); Panamá: *Crosby 4374* (MO); Veraguas: *Nee & Mori 14312* (MO).

World range: Mexico; Central America; Caribbean.

Plants of *Cyclodictyon bicolor* are very much like *C. albicans* in size, leaf shape, and color. Although in Central America *C. bicolor* sometimes occurs in mesic habitats, it is much more commonly found on rocks in and along streams. Its lateral leaves are typically oblong-ovate or oblong and asymmetric and have one margin broadly inflexed, while the dorsal and ventral leaves are ovate and symmetric and have plane margins. The leaf margins in *C. bicolor* are bordered by one to two rows of cells that merge at the apex, and they are usually bluntly serrate to serrulate. The leaf border in *C. bicolor* can at times be very poorly developed and consist almost entirely of one row of cells. Nevertheless, here and there, especially near the apex, the species always has one or more places in which the border is 2-celled. This form of *C. bicolor* is very close to *C. varians*, and it was recognized by Buck (1998) at the species level as *C. albicaule* (Besch.) Kuntze. The leaf cells in *C. bicolor* are enlarged and thin-walled, with the upper cells more or less bulging-hexagonal. Its double costae diverge throughout the leaf and only occasionally do they end in large, projecting, bulbous cells. They are typically entire on the upper dorsal surface, or at times have a few blunt teeth.

In Central America this species belongs to the *Cyclodictyon* group with enlarged, thin-walled, more or less hexagonal upper leaf cells: *C. albicans*, *C. crosbyi*, *C. fendleri*, and *C. varians*. *Cyclodictyon albicans* and *C. fendleri* differ from *C. bicolor* in having much stronger leaf borders that merge into the apex and have the apices filled with elongate cells. In addition, the leaves of *C. bicolor* are strongly serrate, while those of *C. fendleri* are entire or rarely obscurely serrulate. *Cyclodictyon crosbyi* differs from *C. bicolor* in having entire leaf margins; it is also a much smaller species and has asexual propagula at the base of leaves on the dorsal surface. *Cyclodictyon varians* differs from *C. bicolor* in having more or less obsolete leaf borders that are never more than one cell wide. As noted above, special care must be taken when examining collections of the *albicaule*-form of *C. bicolor*, which has very weakly differentiated leaf borders. All collections of *C. bicolor* have at least one place, usually near the apex, in which the leaf border is two cells wide.

3. *Cyclodictyon crosbyi* B. H. Allen, *sp. nov.* Type. Costa Rica. Alajuela: Reserva Biológica de Bosque Nuboso de Monte Verde. Cloud forest area, 0–0.5 km along trail leading SE to Brillante section of reserve; alt. 1500 m, 10°15′N, 85°05′W, 6 May 1975, *Marshall R. Crosby 10025* (MO, holotype).

Species haec a *C. richardsii* foliis ad margines integris vel subintegris et limbatis a 1–2-seriebus cellularum elongatarum cellulisque superis isodiametris differt.

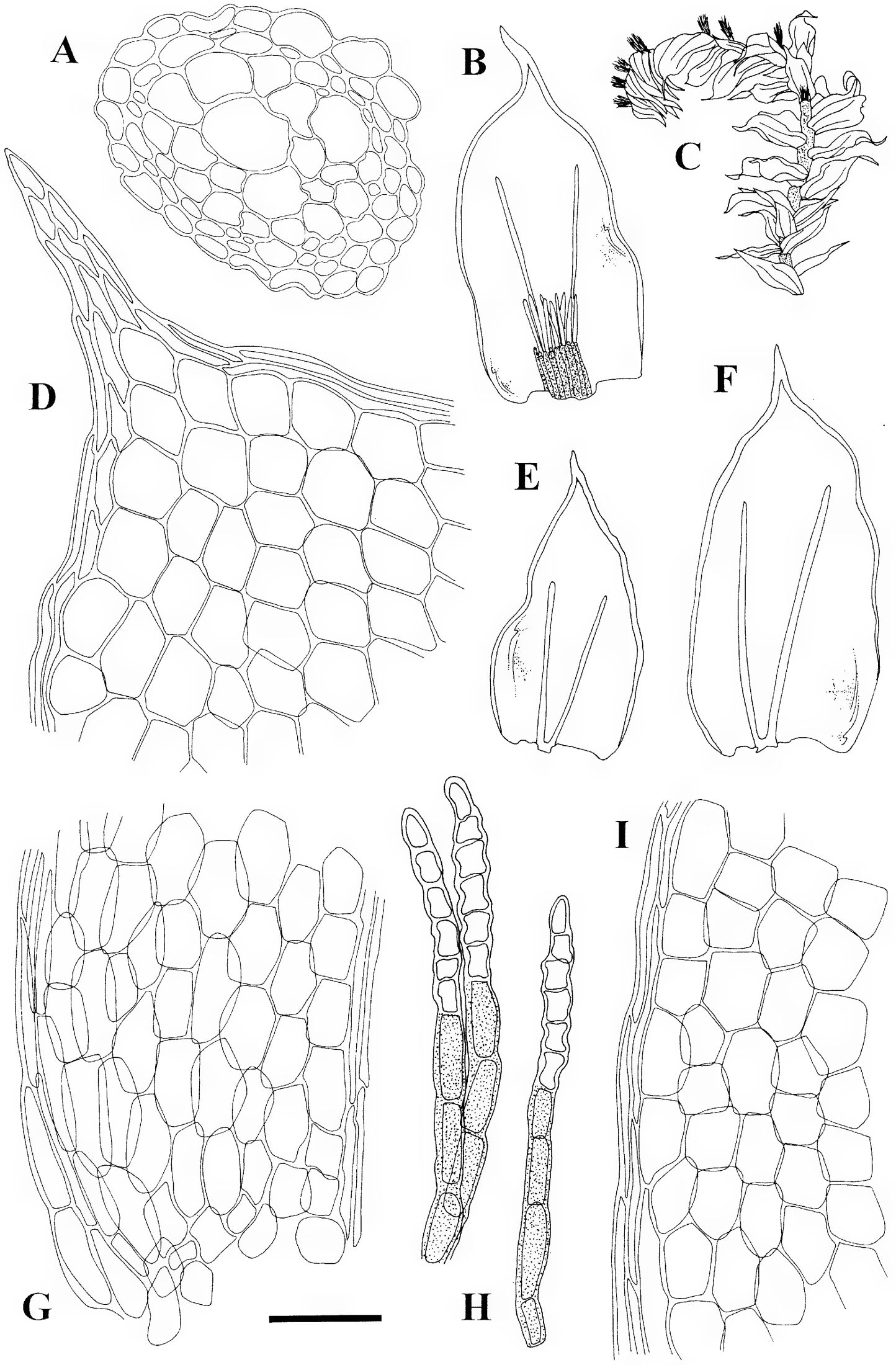
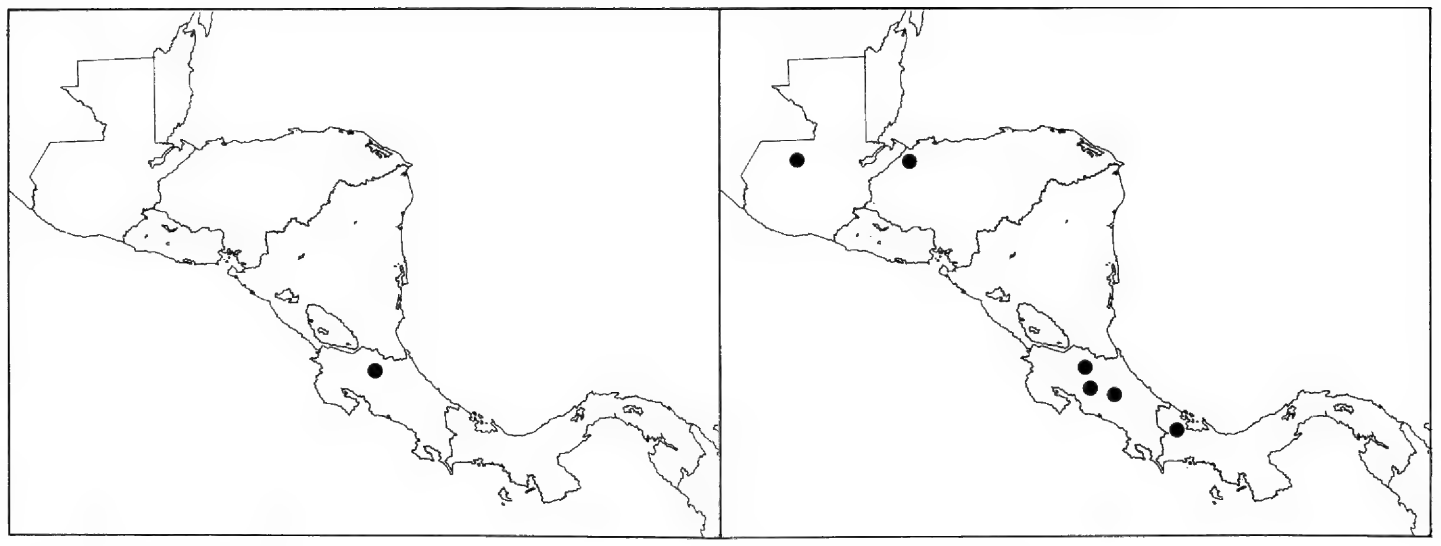


Figure 169. *Cyclodictyon crosbyi*. A. Stem in cross section. B, E & F. Leaves. C. Habit. D. Leaf apex. G. Basal and alar cells. H. Gemmae. I. Median leaf cells and margin. Scale in mm: bar = 0.06 (D, G, I); bar = 0.07 (H); bar = 0.08 (A); bar = 0.28 (B, E, F); bar = 1.3 (C). All figure parts from *Crosby 10025* (type).



Cyclodictyon crosbyi *Cyclodictyon fendleri*

Plants small, 3–6 mm high, pale greenish, in thin mats. Stems prostrate, irregularly branched, hyaline to yellowish when young, becoming reddish with age, somewhat complanate-foliate; stems in cross section with 1-stratose hyalodermis, subepidermis of 1–2 rows of smaller, thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia foliose; axillary hairs fugacious, 2 cells long, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves not or weakly contorted when dry. Lateral leaves spreading when dry, wide-spreading when wet, somewhat asymmetric, ovate, oblong-ovate, or oblong, 0.8–1.0 mm long, abruptly long-acuminate, concave; margins entire or subentire, broadly inflexed below on one side, distinctly bordered by 1–2 rows of narrow, elongate cells confluent in the apices; costae double, ending 2/3–3/4 the leaf length, diverging throughout, at times projecting at the apices and with swollen teeth on upper dorsal surface; cells smooth, upper cells isodiametric, 30–50 µm long, laxly bulging, median and lower cells oblong-rectangular to long-rectangular; alar cells undifferentiated. Ventral and dorsal leaves symmetric, ovate, gradually acuminate; margins plane; costae slender, ending 2/3 the leaf length, not projecting at the tips. Asexual reproduction by light green to brownish filaments at the base of the dorsal surface of the costae and abaxial to the leaf insertions. Dioicous (?). Sporophytes unknown.

Illustration. Figure 169.
Habitat. On rotting tree; 1500 m.
Distribution in Central America. COSTA RICA. Alajuela: *Crosby 10025* (MO).
World range: Central America.

Cyclodictyon crosbyi is a small species with a pale green color, and somewhat crispate leaves when dry. Its lateral leaves are typically oblong-ovate to oblong and asymmetric and have one margin broadly inflexed, while the dorsal and ventral leaves are ovate and symmetric and have plane margins. The leaf margins are distinctly bordered by 1–2 rows of long, narrow cells that merge into a fairly long apex, and they are entire to subentire, although here and there the margins may appear serrulate. The leaf cells are enlarged, bulging, and thin-walled, with isodiametrically hexagonal upper cells. The double costae diverge throughout the leaf, and at times one or both forks end in a large, projecting, bulbous cell. Occasionally, the upper dorsal surface of the costae has swollen teeth. The outstanding feature of *C. crosbyi* is the presence of asexual filaments at the base of the leaves. The filaments occur on the dorsal surface of the costae and on the stems abaxial to the leaf insertion. The initials that give rise to the asexual filaments are identical in form and postion to the rhizoidal intitials.

Cyclodictyon richardsii F. D. Bowers & Magill is a Mexican endemic similar in size to *C. crosbyi*, and the only other Neotropical *Cyclodictyon* species with asexual filaments dorsally at the base of costae. It differs from *C. crosbyi* in having slightly denticulate to serrulate leaves, with 1-celled upper leaf borders and pentagonal to elongate-hexagonal upper leaf cells. Plants of *C. crosbyi* that

lack asexual filaments could be confused with *C. fendleri* or *C. roridum*, because those species have entire to subentire leaf margins. They both, however, are much larger than *C. crosbyi*, with plants that range from 10–40 mm long and leaves that range from 1.0–2.2 mm long. *Cyclodictyon roridum* further differs in having smaller upper leaf cells (18–32 µm vs. 30–50 µm wide) and long, slenderly acuminate to hair-pointed leaves.

4. *Cyclodictyon fendleri* (Müll. Hal.) Broth., Nat. Pflanzenfam. I(3): 935. 1907. *Hookeria fendleri* Müll. Hal., Linnaea 42: 495. 1879. Protologue. Venezuela. [*Fendler*] *Nr. 128*. Type. Musci Fendleriani Venezuelenses. [*Fendler*] *Nr. 128* (FH, isotype).

Hookeria cuspidata Müll. Hal., Syn. Musc. Frond. 2: 189. 1851, illegitimate homonym, not *Hookeria cuspidata* Dozy & Molk., Ann. Sci. Nat., Bot. sér. 3, 2: 305. 1844. *Cyclodictyon cuspidatum* Kuntze, Rev. Gen. Pl. 2: 835. 1891, new name for *Hookeria cuspidata* Müll. Hal. Protologue. Venezuela: *Moritz*, *syn. nov.*

Cyclodictyon lindigianum (Hampe) Kuntze var. *acunae* Thér. *ex* Bizot, Bull. Mens. Soc. Linn. Soc. Bot. Lyon 34: 319. 1965. *Cyclodictyon lindigianum* (Hampe) Kuntze var. *acunae* Thér., Mem. Soc. Cub. Hist. Nat. "Felipe Poey" 14: 233. 1940, invalid name, no Latin description. Protologue. [Cuba] Pic Turquino (*A*[*cuna*] *n*^{o} *286*) Hb. Thériot), *syn. nov.*

Plants small to medium-sized, 1–2 cm long, pale greenish, green, yellowish green, occasionally reddish tinged, in thin or dense mats. Stems prostrate, irregularly branched, hyaline to yellowish when young, becoming reddish with age, somewhat complanate-foliate; stems in cross section with 1-stratose hyalodermis, subepidermis of 1–2 rows of smaller, thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia foliose; axillary hairs fugacious, 2 cells long, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves weakly contorted when dry. Lateral leaves erect-spreading when dry, wide-spreading when wet, asymmetric, oblong-ovate, or oblong, abruptly acuminate, 1.0–1.8 mm long, concave; margins entire to subentire throughout, broadly inflexed below on one side, distinctly bordered by 2–3 rows of narrow, elongate cells confluent in the apices; costae double, weak, ending 2/3–3/4 the leaf length, diverging throughout, occasionally projecting at the apices, smooth on dorsal surface; cells smooth, upper cells broadly hexagonal, 30–60 × 30–40 µm, laxly bulging, median and lower cells oblong-rectangular to long-rectangular; alar cells undifferentiated. Ventral and dorsal leaves symmetric, ovate, gradually acuminate; margins plane; costae slender, ending 2/3 the leaf length, not projecting at the tips. Asexual reproduction absent. Autoicous. Perigonia and perichaetia sessile along stems; perigonia bud-like, 0.6 mm long. Setae elongate, 10–11 mm long, red to red brown, smooth. Capsules inclined to pendent, short-cylindric, neck moderately developed, 1.0–1.5 mm long; exothecial cells at mouth reddish, quadrate to shortly oblate in 2–3 rows, those below red brown, short-rectangular, thick-walled, obscurely collenchymatous; stomata 2–4-celled, rudimentary, on neck; operculum and annulus not seen; peristome diplolepideous; exostome teeth narrowly triangular, with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface dark red, densely and closely striate below, coarsely papillose above, primary walls yellow, smooth, ventral surface hyaline to yellowish, deposition thin, lightly papillose, median lines weak; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not or faintly perforate, cilia absent. Spores not seen. Calyptrae mitrate, yellowish white, irregularly lobed at base, naked, smooth, 2.0 mm long.

Illustrations. Welch (1969, Figs. 55–60 & 77–82, as *C. lindigianum* var. *acunae*); Duarte Bello (1997, Pl. 240 f–h, as *C. lindigianum* var. *acunae*, not Pl. 239, which is *C. varians*). Figure 170.

Habitat. On ground, stream banks, rocks along streams, tree stems, and roots; 850–2134 m.

Distribution in Central America. GUATEMALA. Quiché: *Sharp 2404* (FH). HONDURAS. Cortés: *Allen 14106* (MO). COSTA RICA. Alajuela: *Crosby 10009* (MO); Cartago: *Standley & Valerio 51098* (FH, NY, US); San José: *Bowers 733-g* (MO). PANAMA. Bocas del Toro: *Allen 5639* (MO).

World range: Central America; Caribbean, Western and Northern South America, Brazil.

Cyclodictyon fendleri is a medium-sized species with a pale green color, and slightly crispate leaves when dry. It is very similar to *C. albicans*, and, like that species, it has oblong-ovate to oblong,

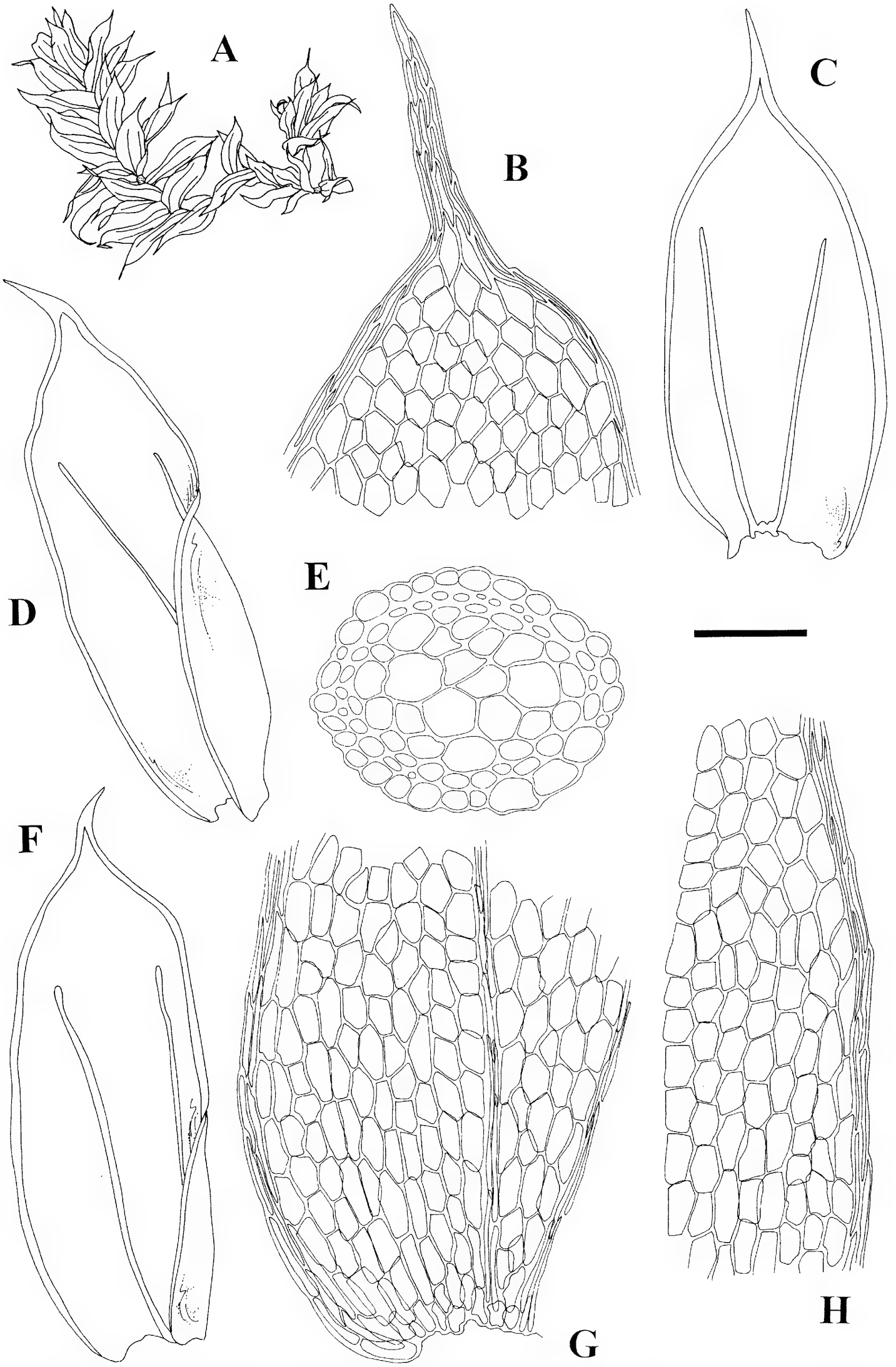


Figure 170. *Cyclodictyon fendleri*. A. Habit. B. Leaf apex. C, D & F. Leaves. E. Stem in cross section. G. Basal and alar cells. H. Median leaf cells and margin. Scale in mm: bar = 0.08 (E); bar = 0.13 (B, G, H); bar = 0.28 (C, D, F); bar = 1.96 (A). All figure parts from *Allen 5639*.

asymmetric lateral leaves with one margin broadly inflexed, and ovate, symmetric dorsal and ventral leaves with plane margins. The leaf margins are strongly bordered by 2–3 rows of cells that merge into a fairly long apex, but, unlike *C. albicans*, the margins are entire to faintly subentire. The leaf cells are enlarged and thin-walled, with the upper cells more or less hexagonal. The double costae are weakly developed and diverge throughout the leaf. The costae only occasionally end in projecting cells, and the dorsal surface is smooth.

This species belongs to the *Cyclodictyon* group with enlarged, thin-walled, more or less hexagonal upper leaf cells: *C. albicans*, *C. bicolor*, *C. crosbyi*, and *C. varians*. Within this group, it appears most closely related to *C. albicans*, which has strongly bordered leaves that are identical to those of *C. fendleri* in shape and in having the apiculus filled with elongate cells. *Cyclodictyon albicans* differs from it in having strongly serrate to serrulate leaf margins. In addition, the costae forks typically end in a projecting, bulbous cell, and they are commonly toothed on the upper dorsal surface. *Cyclodictyon bicolor* differs from *C. fendleri* in having serrate to serrulate leaf margins and weakly developed leaf borders that are often only one cell wide. *Cyclodictyon crosbyi* is similar to *C. fendleri* in having entire leaf margins, but it is a much smaller species and has asexual propagula at the base of leaves on the dorsal surface. *Cyclodictyon varians* differs from *C. fendleri* in having an obsolete leaf border that is never more than one cell wide. *Cyclodictyon roridum* has leaf cells that, although generally smaller, overlap in size with those of *C. fendleri*, and it has entire leaf margins. It is a larger species than *C. fendleri*, and it has more ovate leaves with long-acuminate to hair-pointed leaves. Its upper leaf cells are only 18–32 µm wide.

5. *Cyclodictyon roridum* (Hampe) Kuntze, Revis. Gen. Pl. 2: 835. 1891. *Hookeria rorida* Hampe, Linnaea 32: 155. 1863. Protologue. [Colombia] Bogotá Bogueron ad rupes roridas, 2800 metr., Novbr., [*Lindig*] *no. 59*.

Hookeria capillata Mitt., J. Linn. Soc., Bot. 12: 341. 1869. *Cyclodictyon capillatum* (Mitt.) Kuntze, Revis. Gen. Pl. 2: 835. 1891. Protologue. [Ecuador] Andes Quitenses, Tunguragua loco Mapa-yacu (10,000 ped.), *Spruce, n. 580* foliis integerrimis, et *Spruce, n. 581* foliis serrulatis. [Colombia] Nova Granata, Bogotá loco Boqueron (8600 ped.) ad ramulos emortuos in stillicidiis, *Weir, n. 331, 337, et 367*, omnia foliis serrulatis. Type (see Buck 1987). *Weir 331* (NY, lectotype).

Hookeria obliquicuspis Müll. Hal., Bull. Herb. Boissier 5: 564. 1897. *Cyclodictyon obliquicuspis* (Müll. Hal.) H. A. Crum & E. B. Bartram, Bull. Inst. Jamaica, Sci. Ser. 8: 50. 1958. Protologue. Jamaica, Newhaven Pass, 5600 ped alt., inter *Microthamnium frustula* pauca: *W. Harris* Decembri 1896 sub *N° 10097* Hb. Jamaicensis.

Plants medium-sized, 1–4 cm long, green, yellowish green, or reddish yellow, in thin or dense mats. Stems prostrate, irregularly branched, hyaline to yellowish when young, becoming reddish with age, somewhat complanate-foliate; stems in cross section with 1-stratose hyalodermis, subepidermis of 1–2 rows of smaller, thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia foliose; axillary hairs fugacious, 2–3 cells long, basal cell short-rectangular, reddish brown, upper cell(s) oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves variably contorted when dry. Lateral leaves erect-spreading when dry, wide-spreading when wet, asymmetric, oblong-lanceolate to ovate-lanceolate, 1.5–2.2 mm long, abruptly slenderly long-acuminate to hair-pointed, concave; margins entire to subentire throughout, broadly inflexed below on one side, distinctly bordered by 2–3 rows of narrow, elongate cells confluent in the apices; costae double, weak, ending 2/3–3/4 the leaf length, diverging throughout, occasionally projecting at the apices, smooth on dorsal surface; cells smooth, upper cells irregularly shaped, hexagonal to elongate-hexagonal, 22–34 × 18–32 µm, laxly bulging, median and lower cells oblong-rectangular to long-rectangular; alar cells undifferentiated. Ventral and dorsal leaves symmetric, ovate, abruptly slenderly long-acuminate to hair-pointed; margins plane; costae slender, ending 2/3 the leaf length, not projecting at the tips. Asexual reproduction absent. Autoicous. Perigonia and perichaetia sessile along stems; perigonia bud-like, 0.6 mm long. Setae elongate, 10–20 mm long, red to red brown, flexuose, smooth. Capsules inclined to horizontal, short-cylindric, neck moderately developed, 1.5–2.0 mm long; exothecial cells at mouth reddish, quadrate to shortly oblate in 2–3 rows, those below red brown, short-rectangular, with thick-vertical walls and thinner horizontal walls, obscurely collenchymatous;

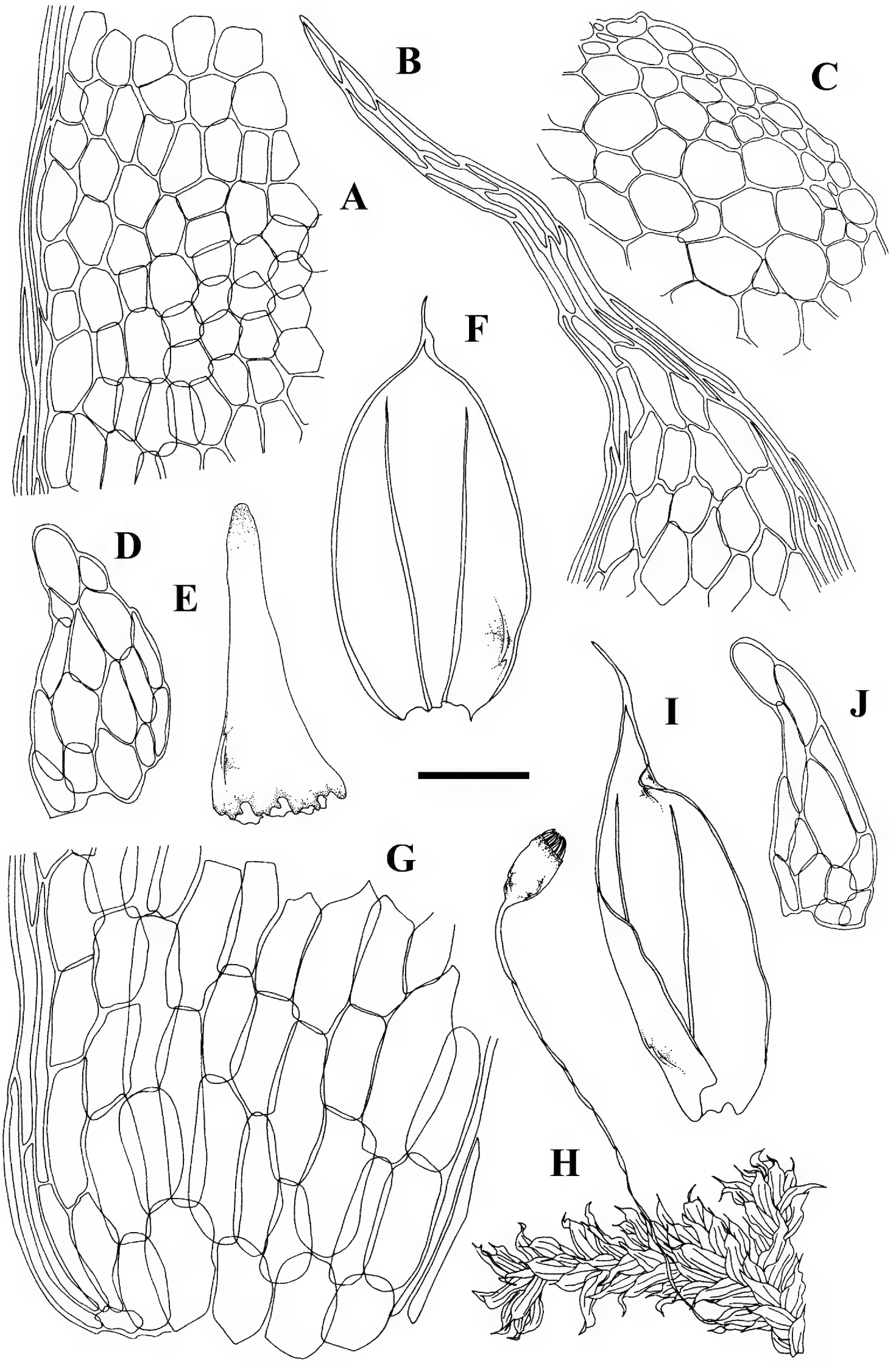
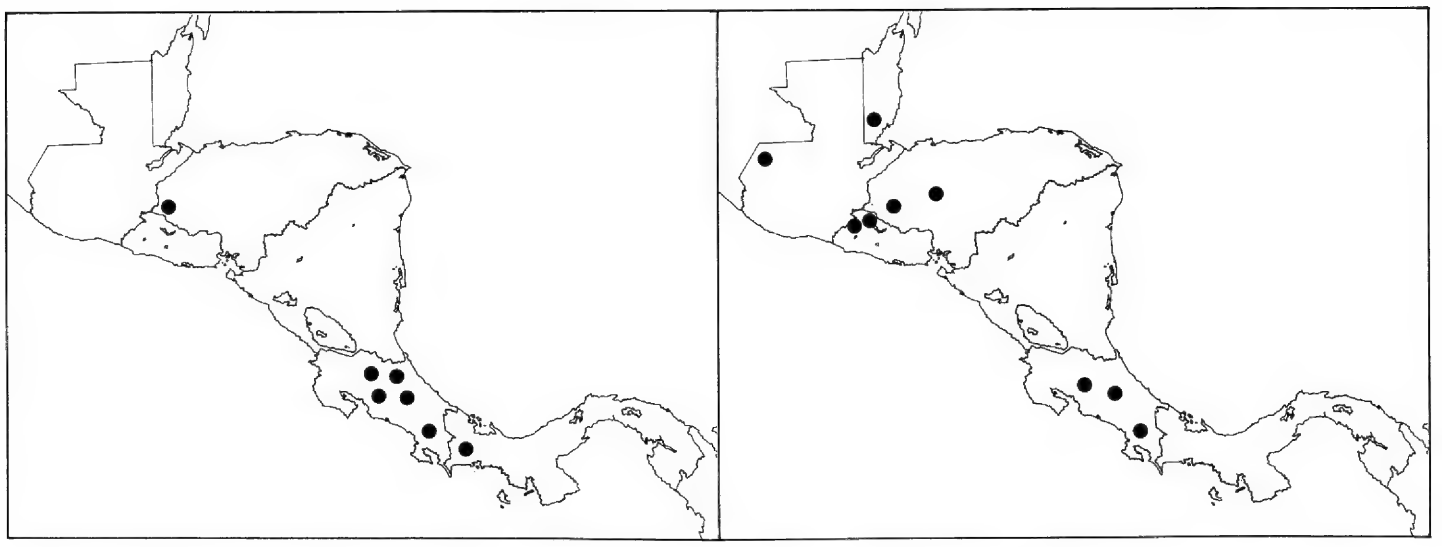


Figure 171. *Cyclodictyon roridum*. A. Median leaf cells and margin. B. Leaf apex. C. Stem in cross section. D & J. Pseudoparaphyllia. E. Calyptra. F & I. Leaves. G. Basal and alar cells. H. Habit. Scale in mm: bar = 0.06 (A, B, D, G); bar = 0.08 (C); bar = 0.5 (F, I); bar = 0.9 (E); bar = 2.5 (H). H from *Crosby 5992*; all other figure parts from *Crosby 10001*.



Cyclodictyon roridum *Cyclodictyon rubrisetum*

stomata 2–4-celled, rudimentary, on neck; opercula long-rostrate, 1.5–2.0 mm long; annuli rudimentary, deciduous; peristome diplolepideous; exostome teeth narrowly triangular, with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface dark red, densely and closely striate below, coarsely papillose above, primary walls yellow, smooth, ventral surface hyaline to yellowish, deposition thin, lightly papillose, median lines weak; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not or faintly perforate, cilia absent. Spores 12–16 µm, lightly roughened. Calyptrae mitrate, yellowish white, irregularly lobed at base, naked, smooth, 1.5–2.0 mm long.

Illustrations. Churchill and Linares (1995, Fig. 38 e–g); Buck (1998, Pl. 11 1–3); Gradstein *et al.* (2001, Fig. 165 H–K). Those in Bartram (1949, Fig. 133 G & H), Welch (1966, Figs. 106–115), and Sharp *et al.* (1994, Fig. 588) as *C. roridum* are *C. subtortifolium*. Figure 171.

Habitat. On moist humus, tree bases, exposed roots, rotting wood, and twigs; 1500–2500 m.

Distribution in Central America. HONDURAS. Ocotepeque: *Allen 14456* (MO). COSTA RICA. Alajuela: *Crosby 10001* (MO); Cartago: *Crosby & Crosby 5909* (MO); Heredia: *Crosby 13129* (MO); Puntarenas: *Dauphin 1387* (MO); San José: *Crosby & Crosby 5829* (CR, MO). PANAMA. Chiriquí: *Crosby 3988* (MO).

World range: Central America; Caribbean, Western South America.

Cyclodictyon roridum is a medium-sized species with a green to yellowish red color, and somewhat crisped leaves when dry. It has oblong-lanceolate to ovate-lanceolate, asymmetric lateral leaves, with one margin broadly inflexed, and ovate, symmetric dorsal and ventral leaves, with plane margins. The leaf margins are strongly bordered by 2–3 rows of cells that merge into a long, slender (sometimes hair-pointed) acumina. Most Central American material of *C. roridum* is similar to Caribbean material of the species in having entire to faintly subentire leaf margins, but some collections, like those from South America, have serrulate leaf margins. The upper cells are irregularly hexagonal, mostly as wide as long, thin-walled, and enlarged. The double costae are weakly developed and diverge throughout the leaf. The costae only occasionally end in projecting cells, and the dorsal surface is smooth.

Although *C. roridum* has large leaf cells, they are relatively small when compared to other members of the hexagonal-celled group of species (*C. albicans*, *C. bicolor*, *C. fendleri*, *C. crosbyi*, *C. varians*), which generally have leaf cells 30–60 µm wide. It should be noted, however, that the range of its leaf cell widths overlaps with the range of that group. The species also differs from that group of species in having more elongate, thin, and bulging basal leaf cells. *Cyclodictyon roridum* further differs from all members of the group except *C. fendleri* and *C. crosbyi* in having entire or subentire leaf margins. In addition to its wider leaf cells, *C. fendleri* is a much smaller species than *C. roridum*, with oblong-ovate or oblong, apiculate to cuspidate leaves, while *C. crosbyi* is an even smaller species with rhizoidal gemmae. *Cyclodictyon albicans* further differs from *C. roridum* in having costae that typi-

cally end in a projecting, bulbous cell, and the costae are commonly toothed on the upper dorsal surface. *Cyclodictyon bicolor* also differs from *C. roridum* in having weakly developed leaf borders that are often only one cell wide. *Cyclodictyon varians* differs from *C. roridum* in having an obsolete leaf border that is never more than one cell wide.

Cyclodictyon roridum has been confused with two aquatic to semiaquatic species: *C. subtortifolium* and *Lepidopilum tortifolium.* In addition to its aquatic habitat, *C. subtortifolium* differs from *C. roridum* in having serrulate leaves that are strongly bordered by 4–7 rows of cells. *Lepidopilum tortifolium* differs from *C. roridum* in having short leaf apices that are filled with short rather than elongate cells, and longer upper leaf cells.

6. *Cyclodictyon rubrisetum* (Mitt.) Kuntze, Revis. Gen. Pl. 2: 835. 1891. *Hookeria rubriseta* Mitt., J. Linn. Soc., Bot. 12: 341. 1869. Protologue. [Colombia] Andes Bogotenses, *Weir*. Type. Colombia. Andes of Bogotá, *Weir* (NY, holotype).

Cyclodictyon erubescens E. B. Bartram, Bryologist 49: 118. 1946. Protologue. Guatemala. Dept. Huehuetenango: Cerro Victoria, Sierra de los Cuchumatanes, near Barillas, alt. 1800–2000 m, *Steyermark 49760.* Types. Guatemala. Dept. Huehuetenango: Cerro Victoria, Sierra de los Cuchumatanes, near Barillas, alt. 1800–2000 m, July 29 1942, *Julian A. Steyermark 49760* (F, NY, isotypes).

Plants medium-sized, 1–3 cm long, red to reddish purple, tinged with green, in thin mats. Stems prostrate, irregularly branched, yellowish when young, red with age, weakly complanate-foliate; stems in cross section with 1-stratose hyalodermis, subepidermis of 1–2 rows of smaller, thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia foliose; axillary hairs 2 cells long, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves somewhat contorted and undulate at the margins, flexuose when dry, wide-spreading when wet, asymmetric, oblong to oblong-ovate, or oblong-lanceolate, 1.5–2.5 mm long, abruptly acuminate, long, slenderly pointed, concave; margins entire to subentire throughout, broadly inflexed below on one side, distinctly bordered by 2–3 rows of narrow, elongate cells, confluent in the apices; costae double, weak, ending 2/3–3/4 the leaf length, diverging throughout, not projecting at the apices, smooth on dorsal surface; cells smooth, upper cells oval-hexagonal, 30–50 × 14–24 µm, laxly bulging, median and lower cells oblong-rectangular to long-rectangular; alar cells undifferentiated. Asexual reproduction absent. Dioicous. Setae elongate, 13–20 mm long, red to red brown, smooth. Capsules inclined to pendent, short-cylindric, neck moderately developed, 1.5–2.0 mm long; exothecial cells at mouth reddish, quadrate to shortly oblate in 2–3 rows, those below red brown, short-rectangular, obscurely collenchymatous, longitudinal walls thick, horizontal walls thin; stomata 2–4-celled, rudimentary, on neck; opercula long-rostrate, 1.0–1.2 mm long; annuli rudimentary; peristome diplolepideous; exostome teeth narrowly triangular, median furrows broad, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface dark red, densely and closely striate below, coarsely papillose above, primary walls yellow, smooth, ventral (inner) surface hyaline to yellowish, deposition thin, lightly papillose, median lines weak; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, keeled, not or faintly perforate, cilia absent. Spores 10–14 µm, smooth to lightly roughened. Calyptrae mitrate, yellowish white, irregularly lobed at base, naked, smooth, 2.0 mm long.

Illustrations. Bartram (1949, Fig. 134 D & E, as *C. erubescens*); Welch (1966, Figs. 89–97, as *C. erubescens*; Figs. 116–121); Sharp *et al.* (1994, Fig. 587, as *C. erubescens*); Churchill and Linares (1995, Fig. 38 c & d). Figure 172.

Habitat. Terrestrial, on rotting logs, roots, or limestone outcrops, also epiphytic; 710–3000 m.

Distribution in Central America. BELIZE. Toledo: *Allen 18650* (MO). GUATEMALA. Huehuetenango: *Steyermark 49760* (F, NY). EL SALVADOR. Chalatenango: *Sipman et al. 37806* (NY); Santa Ana: *Watson ES-0100* (MO). HONDURAS. Comayagua: *Allen 12307* (MO); Lempira: *Allen 11318* (MO). COSTA RICA. Cartago: *Gómez 19597* (MO); Puntarenas: *Crosby 2672* (MO); San José: *Bowers 210* (MO, NY).

World range: Mexico, Central America; Western South America.

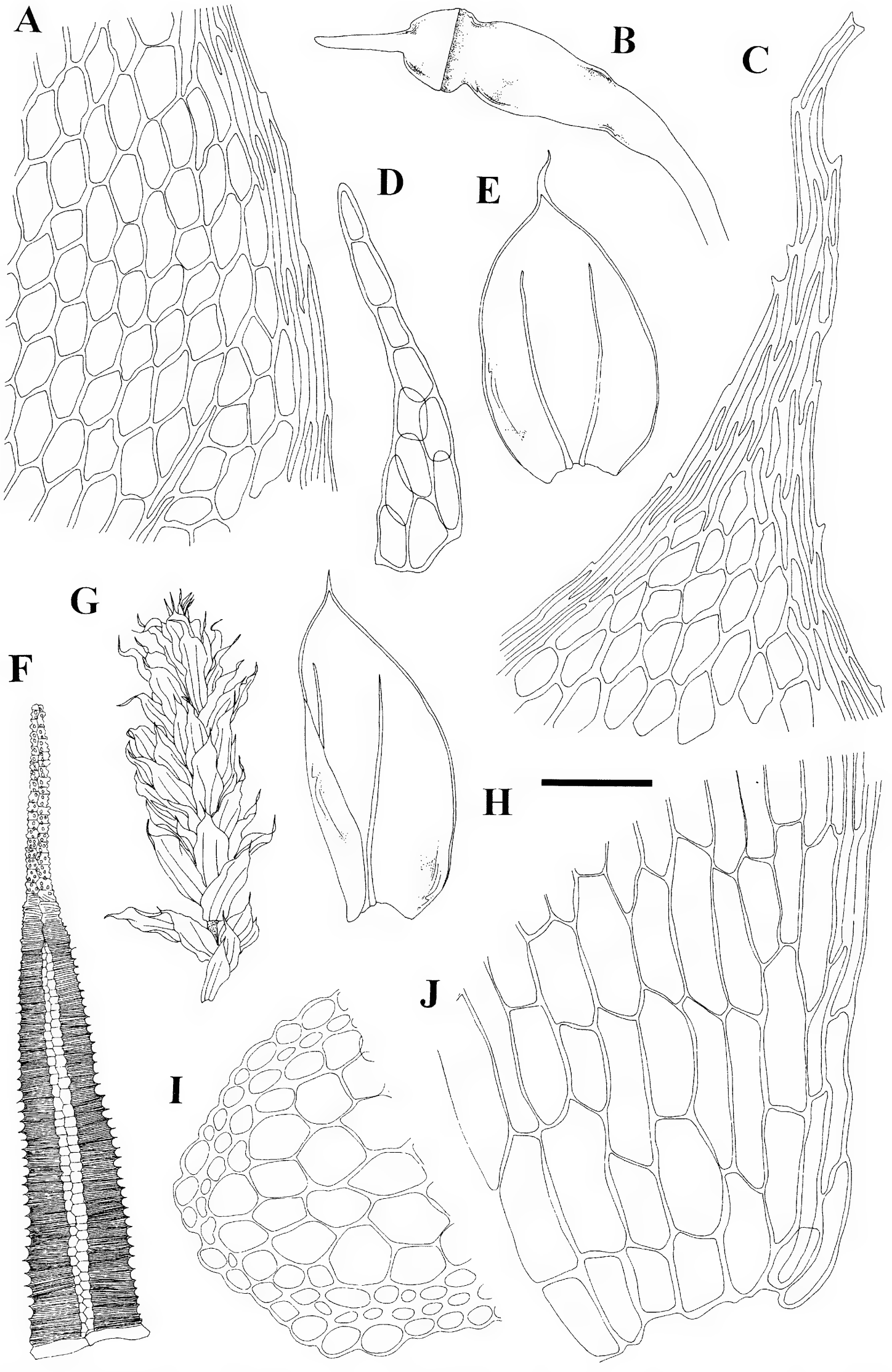


Figure 172. *Cyclodictyon rubrisetum*. A. Upper leaf cells and margin. B. Seta, capsule, and operculum. C. Leaf apex. D. Pseudoparaphyllia. E & H. Leaves. F. Exostome, dorsal (outer) surface. G. Habit. I. Stem in cross section. J. Basal and alar cells. Scale in mm: bar = 0.06 (A, C, D, J); bar = 0.08 (I); bar = 0.09 (F); bar = 0.6 (E, H); bar = 0.9 (B); bar = 1.96 (G). D, E, H, I from *Allen 11318*; B, F from *Watson ES-0100*; all other figure parts from *Steyermark 49760*.

Cyclodictyon rubrisetum is a medium-sized species that in Central America usually has purplish red or reddish tinged plants. Occasionally its plants are yellowish green with a weak reddish hue. It has oblong to oblong-ovate leaves that are erect-flexuose when dry, end in long, slender points, and typically have undulate margins. The strongly bordered margins are usually entire or subentire, but occasionally the leaves are serrulate at the tips. In contrast, leaves on the type from Colombia have more consistently serrulate to serrate leaf margins. The upper leaf cells in *C. rubrisetum* are variably shaped, and usually some of them are longer than wide, while others are isodiametric. The sporophytes of *C. rubrisetum* are more or less identical to the sporophytes found throughout *Cyclodictyon*.

Bartram (1949) confused *C. rubrisetum* with the form of *C. albicans* that often has long upper leaf cells. All forms of *C. albicans* differ from *C. rubrisetum* in having a pale green to green color; smooth leaves with consistently serrate to serrulate leaf margins; broader upper leaf cells; and costae that project at the tips and are usually toothed at back. In contrast, *C. rubrisetum* is a reddish plant, with leaves that are often undulate when dry, entire or subentire leaf margins, narrower and longer upper leaf cells, and weak costae that are smooth on the dorsal surface and do not project at the tips.

In Central America *C. crosbyi*, *C. fendleri*, and *C. roridum* could be confused with *C. rubrisetum* because they all have entire to subentire leaf margins. *Cyclodictyon rubrisetum*, however, is the only member in that group with a reddish coloration. *Cyclodictyon crosbyi* further differs from *C. rubrisetum* in its smaller size (plants only 3–6 mm high) and in having asexual filaments at the base of its leaves. *Cyclodictyon fendleri* also differs from *C. rubrisetum* in having narrower, apiculate to cuspidate leaves and wider upper leaf cells (30–60 µm vs. 14–24 µm). *Cyclodictyon roridum* and *C. rubrisetum* are very similar and both species have long pointed leaf apices. *Cyclodictyon roridum* differs from *C. rubrisetum* only in its yellowish green color; broader, often ovate leaves that lack undulate margins; and more consistently isodiametric laminal cells.

7. *Cyclodictyon subtortifolium* (E. B. Bartram) W. R. Buck, Brittonia 39: 22. 1987. *Lepidopilum subtortifolium* E. B. Bartram, Bryologist 49: 119. 1946. Protologue. Guatemala. Dept. San Marcos: along road between San Sebastián at km 21 and km 8, 8–18 miles northwest of San Marcos, alt. 2700–3800 m, *Steyermark 35714* type, also *36928*. Type. Guatemala. Volcán Tajumulco. Dept. San Marcos: along road between San Sebastián at km 21 and km 8, 8–18 miles northwest of San Marcos, alt. 2700–3800 m, Feb. 15, 1940, *Julian A. Steyermark 35714* (F, isotype).

Amblytropis denticulata Thér., Mem. Soc. Cub. Hist. Nat. "Felipe Poey" 14: 367. 1940, not *Cyclodictyon denticulatum* Kuntze, Revis. Gen. Pl. 2: 835. 1891. *Lepidopilum denticulatum* (Thér.) F. D. Bowers *in* Sharp *et al.*, Mem. New York Bot. Gard. 69: 801. 1994. Protologue. [Cuba] Pico Turquiño (*Acuña 391*).

Amblytropis pocsii Duarte Bello, Acta Bot. Cub. 13: 1. 1982. Protologue. [Cuba] Submersae et affixae ad rupes alveis rivuli, *Duarte 3743* [leg. Pócs 9066/CC]. Type. Cuba. Oriente: Prov. Granma. Sierra Maestra cerca Pico Bayamesa. Fangales humedas de la Subida Albear, en alt. 1300–1400 m. Sobre rocas sumergidas, 30 Nov. 1978, Col. *T. Pócs No. 9066/CC* (MO, isotype).

Plants small to medium-sized, 10–40 mm long, pale, yellowish green, or reddish yellow, in thin mats. Stems prostrate, irregularly branched, hyaline to yellowish when young, becoming reddish with age, somewhat complanate-foliate; stems in cross section with weakly differentiated 1–3-stratose hyalodermis, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia foliose; axillary hairs fugacious, 2 cells long, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids sparse, from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves contorted when dry, widespreading when wet. Lateral leaves asymmetric, oblong to oblong-ovate, 1.5–2.5 mm long, short-acuminate, concave; margins serrate to denticulate, broadly inflexed below on one side, strongly bordered by 4–7 rows of narrow, elongate cells, confluent in the apices; costae double, ending 2/3–7/8 the leaf length, diverging throughout, occasionally projecting at the apices, smooth on dorsal surface, often confluent with leaf border on one side; cells smooth, upper cells irregularly rounded-hexagonal, 8–28 × 12–20 µm, laxly bulging, median and lower cells oblong-rectangular to long-rectangular; alar cells undifferentiated. Ventral and dorsal leaves symmetric, ovate. Asexual reproduction absent. Dioicous. Perigonia sessile on stems, bud-like, 1 mm long. Perichaetia and sporophytes unknown.

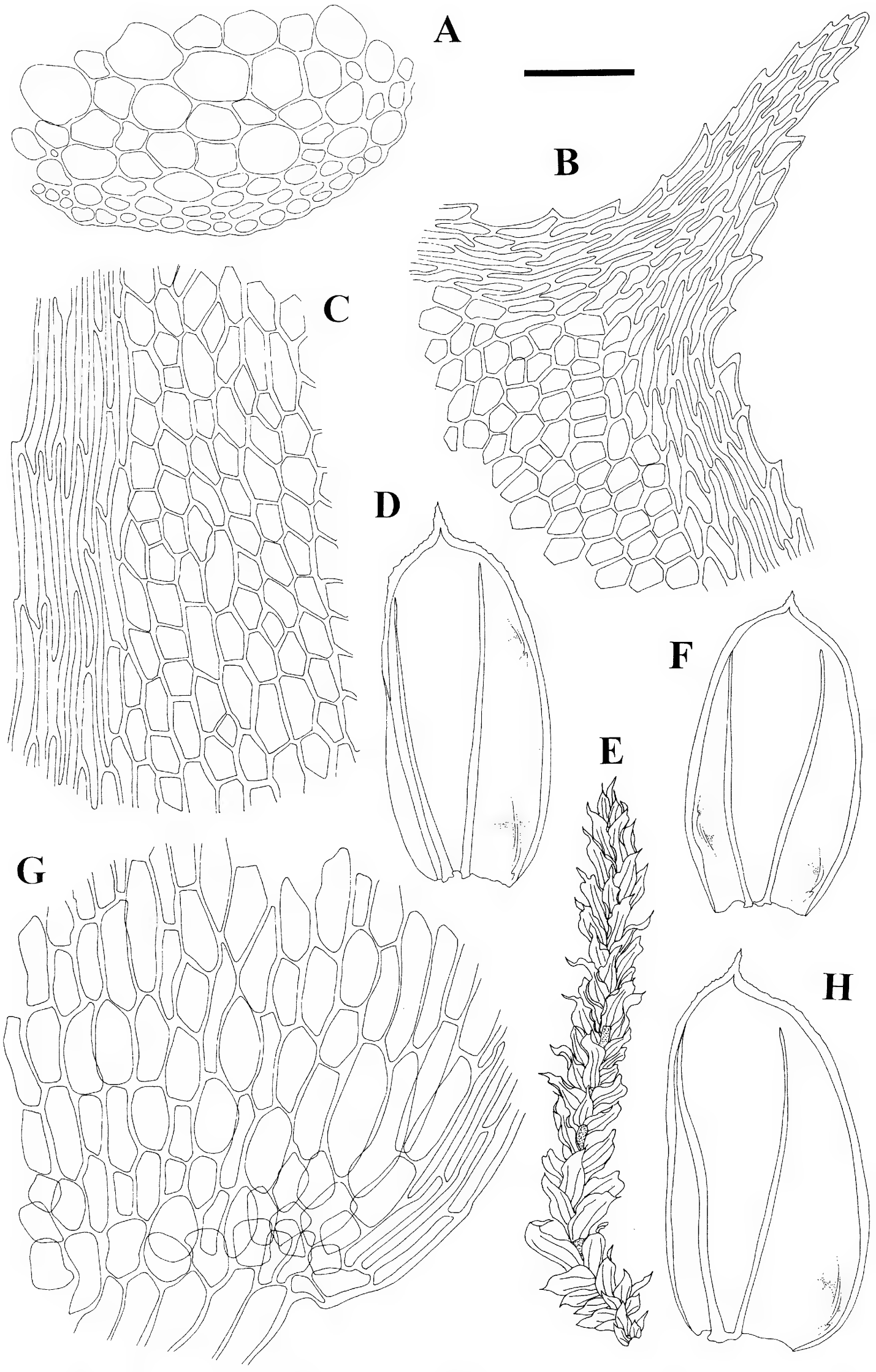
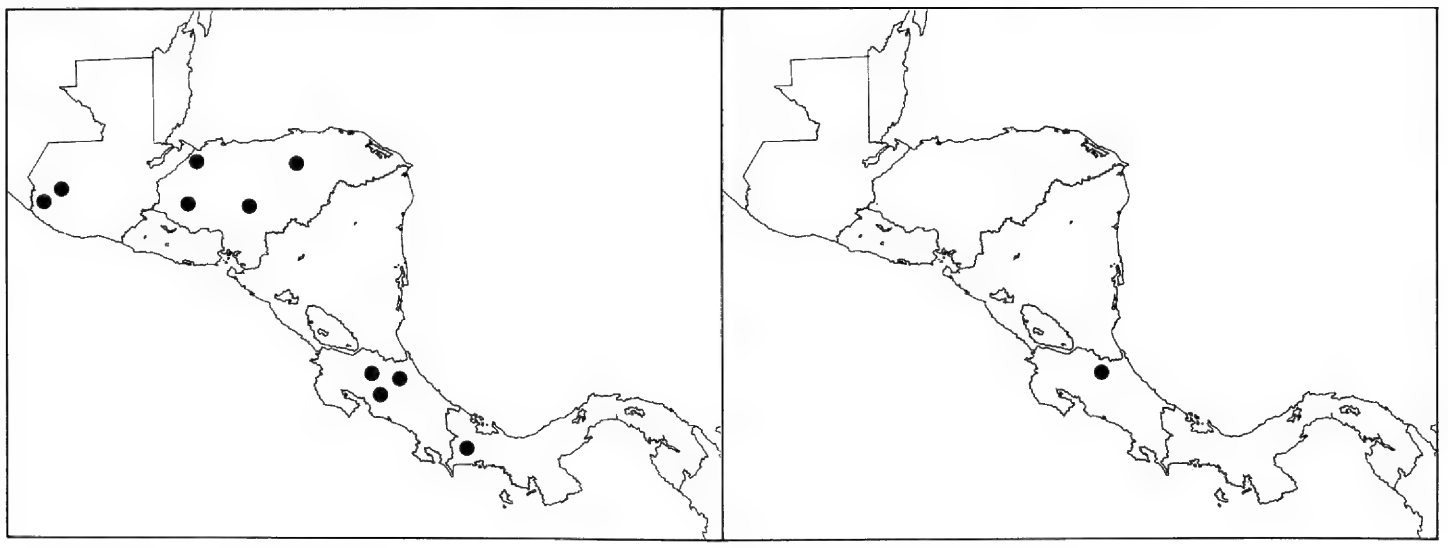


Figure 173. *Cyclodictyon subtortifolium*. A. Stem in cross section. B. Leaf apex. C. Median leaf cells and margin. D, F & H. Leaves. E. Habit. G. Basal and alar cells. Scale in mm: bar = 0.06 (B, C, G); bar = 0.08 (A); bar = 0.6 (D, F, H); bar = 3.2 (E). All figure parts from *Steyermark 35714* (type).



Cyclodictyon subtortifolium *Cyclodictyon validirugosum*

Illustrations. Bartram (1949, Fig. 133 G & H, as *Cyclodictyon roridum*; Fig. 141 A–C, as *Lepidopilum subtortifolium*); Welch (1966, Figs. 106–115, as *C. roridum*); Welch (1971a, Figs. 1–11); Sharp *et al.* (1994, Fig. 588, as *C. roridum*; Fig. 601, as *Lepidopilum denticulatum*); Duarte Bello (1997, Pl. 218, as *Amblytropis denticulata*; Pl. 219, as *Amblytropis pocsii*); Buck (1998, Pl. 11 1–7). Figure 173.

Habitat. On rocks in streams and in waterfalls, occasionally on very wet bark or epiphyllous at tips of fern pinnae; 900–2800 m.

Distribution in Central America. GUATEMALA. Quetzaltenango: *Steyermark 34926* (F, FH); San Marcos: *Steyermark 36902* (F, FH, NY). HONDURAS. Cortés: *Allen 14114* (MO, TEFH); Francisco Morazán: *Davidse & House 34222A* (MO); Lempira: *Allen 12017* (MO); Olancho: *Allen 12595* (MO). COSTA RICA. Alajuela: *Crosby & Crosby 5898* (MO); Heredia: *Crosby & Crosby 6018* (MO); San José: *Stiles & Marin 42* (US). PANAMA. Chiriquí: *D'Arcy* (MO).

World range: Mexico; Central America; Caribbean; Western South America.

Cyclodictyon subtortifolium is a rheophytic species, with contorted leaves, small, more or less isodiametric leaf cells, and strongly developed leaf borders. It is the only Central American species of *Cyclodictyon* with leaves consistently bordered by four or more rows of elongate cells. The leaf margins are serrate or dentate, and often the teeth are enlarged or somewhat inflated. When well developed, the leaf borders merge in the apex and completely fill the long apiculus. The species, however, is variable in this respect and some leaves have the apex filled with considerably shorter cells (see, *e.g.*, Fig. 588 C in Sharp *et al.* 1994). The Mexican endemic, *Cyclodictyon arsenei* Thér., is the only regional *Cyclodictyon* species that can be confused with *C. subtortifolium*, because they both have broadly bordered leaves. It differs from *C. subtortifolium* only in having somewhat elongate rather than isodiametric upper leaf cells.

Cyclodictyon roridum has been chronically confused with *C. subtortifolium*, *e.g.*, the treatments of *C. roridum* in Bartram (1946) and Welch (1966) are based on collections of *C. subtortifolium*. *Cyclodictyon roridum* is a terrestrial species with long, narrowly acuminate to hair-pointed, entire-margined leaves. Its leaf borders are never more than 2–3 cells wide. *Lepidopilum tortifolium* is much more likely to be confused with *C. subtortifolium*, since both are aquatic species with leaves that are strongly contorted when dry. *Lepidopilum tortifolium* is usually a larger plant than *C. subtortifolium* and its more strongly asymmetric lateral leaves are often obovate. Furthermore, *L. tortifolium* has weaker costae (1/2–2/3 vs. 2/3–7/8 the leaf length) that never project at the apex and larger (40–60 × 25–35 µm vs. 8–28 × 12–20 µm) upper leaf cells. In addition, the leaf border in *L. tortifolium* is weaker than in *C. subtortifolium*, it is not confluent at the apex, and it is consistently filled with short cells.

8. *Cyclodictyon validirugosum* B. H. Allen, *sp. nov*. Type. Costa Rica. Heredia: Immediate vicinity of Laguna Barba. Alt. ca. 2600 m. 1 May 1975, 10°05′N, 083°55′W, *Marshall R. Crosby 10938* (MO, holotype; BM, CR, DUKE, F, FH, G, H, NY, PMA, US, isotypes).

Inter omnia species *Cyclodictyi* plantis celsis et longioribus, latioribus, valde rugosis foliis differt.

Plants medium-sized to large, 5–10 cm long, yellowish green, in loose mats. Stems prostrate, irregularly branched, yellowish, becoming reddish with age, somewhat complanate-foliate; stems in cross section when young with all cells homogeneously thin-walled, when old with 1-stratose hyalodermis, epidermis of 1–2 rows of smaller, thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs fugacious, 2–3 cells long, basal cell short-rectangular, reddish brown, upper cell(s) oblong-elongate, hyaline; rhizoids not seen. Leaves erect to laxly imbricate, strongly crispate and undulate above when dry or wet. Lateral leaves somewhat asymmetric, ovate-lanceolate, 3.5–4.0 × 1.4–1.6 mm, constricted at about 3/4 the leaf length, narrowly acute, concave, not decurrent; margins entire throughout, occasionally obscurely serrulate, strongly bordered by 2–3(–4) rows of narrow, elongate cells, plane; costae double, weak, 2 cells thick, gradually divergent, 2/3–3/4 the leaf length; cells smooth, upper and median cells broadly hexagonal to elongate-hexagonal, 40–70 × 24–30 µm, laxly bulging; basal cells oblong-rectangular to long-rectangular, 80–140 × 30–50 µm; alar cells undifferentiated. Ventral and dorsal leaves symmetric, ovate, not constricted, gradually acuminate. Dioicous. Setae elongate, 30–35 mm long, red to red brown, smooth. Capsules inclined, short-cylindric, neck moderately developed, 1.5–2.0 mm long; exothecial cells at mouth reddish, quadrate to shortly oblate in 2–3 rows, those below oblong to short-rectangular, somewhat collenchymatous; stomata 2–4-celled, rudimentary, on neck; operculum and annulus not seen; peristome diplolepideous; exostome teeth narrowly triangular, with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface dark red, densely and closely striate below, coarsely papillose above, primary walls yellow, smooth, ventral (inner) surface hyaline to yellowish, deposition thin, lightly papillose, median lines weak; endostome as long as the exostome, yellow, papillose throughout, basal membranes high, segments broad, strongly keeled, not or faintly perforate, cilia absent. Spores 12–16 µm, smooth to lightly roughened. Calyptra not seen.

Illustration. Figure 174.

Habitat. On ground; 1850–2700 m.

Distribution in Central America. COSTA RICA. Heredia: *Valerio 52* (NY, US), *Crosby 10937A* (MO).

World range: Central America.

Cyclodictyon validirugosum is a medium-sized to large species presently known only from the Costa Rican province of Heredia. It has laxly erect, somewhat complanate, very long, ovate-lanceolate leaves that are strongly crispate and undulate, whether wet or dry, and never reddish tinged. The leaf margins are entire and bordered by mostly three rows of long, narrow cells. The leaves of *C. validirugosum* are somewhat constricted at the base of the acumina, and this, in combination with its enlarged, laxly bulging lower leaf cells, gives the plants an aspect similar to *Amblytropis*. However, it differs fundamentally from *Amblytropis* in having exostome teeth that are strongly cross-striate on the lower dorsal surface. There is no other Central American species of *Cyclodictyon* remotely similar to *C. validirugosum* in overall aspect, plant size, as well as leaf size and shape. At first glance, plants of *C. validirugosum* appear very close to those of *Thamniopsis undata*, because they are similar in size, leaf shape, and in having strongly undulate leaves. *Thamniopsis undata* differs from *C. validirugosum* in having elimbate, strongly serrate leaf margins.

9. *Cyclodictyon varians* (Sull.) Kuntze, Revis. Gen. Pl. 2: 835. 1891. *Hookeria varians* Sull., Proc. Amer. Acad. Arts 5: 285. 1861. Protologue. [Cuba] Logs in dense woods, [*Wright*] *88*.

Plants medium-sized, 10–30 mm long, pale green or yellowish green, in thin or dense mats. Stems prostrate, irregularly branched, hyaline to yellowish when young, becoming reddish with age, com-

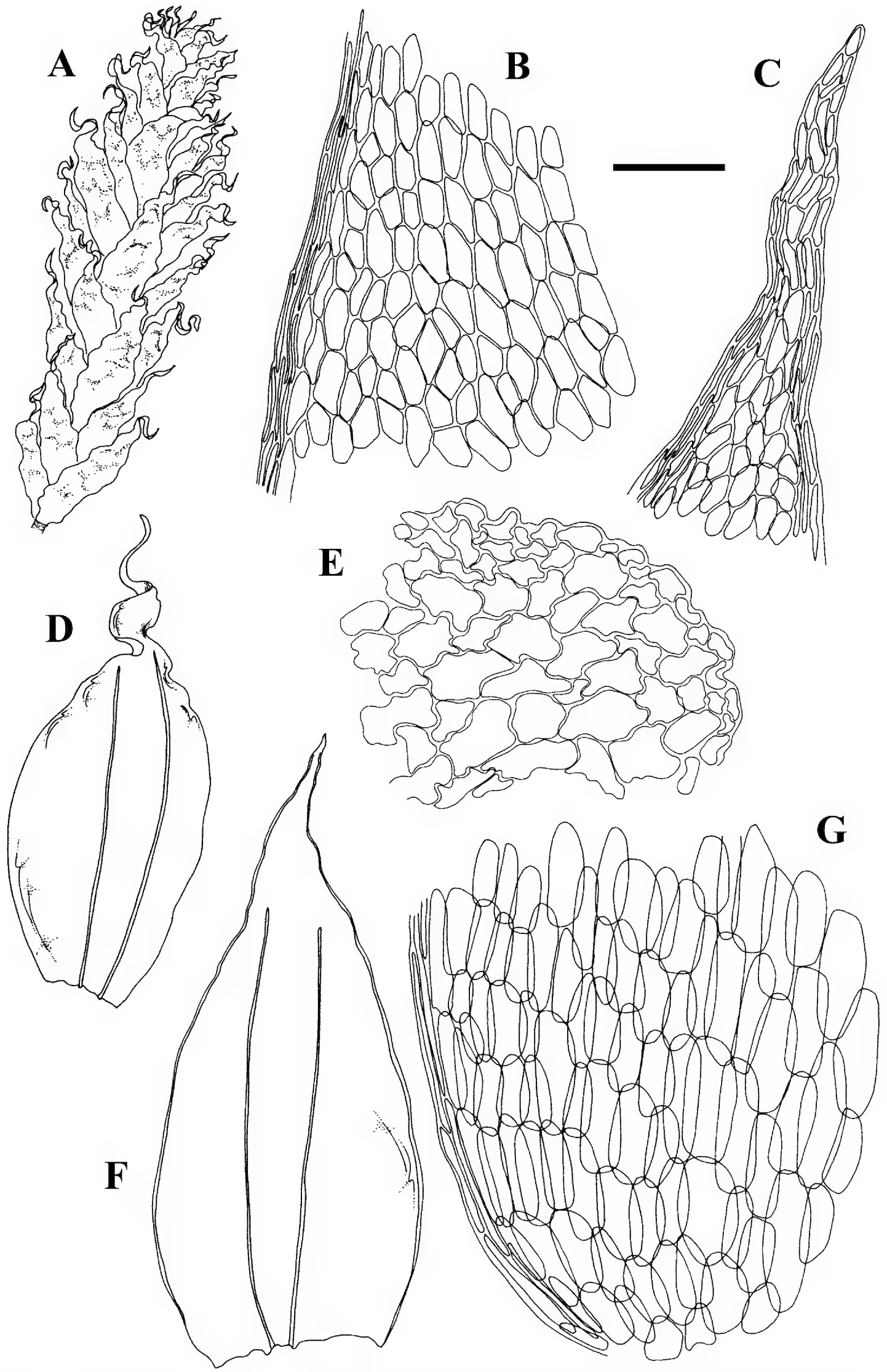


Figure 174. *Cyclodictyon validirugosum*. A. Habit. B. Median leaf cells. C. Leaf apex. D & F. Leaves. E. Stem in cross section. G. Basal and alar cells. Scale in mm: bar = 0.08 (E); bar = 0.13 (B, C, G); bar = 0.71 (D, F); bar = 2.0 (A). All figure parts from *Valerio 52*.

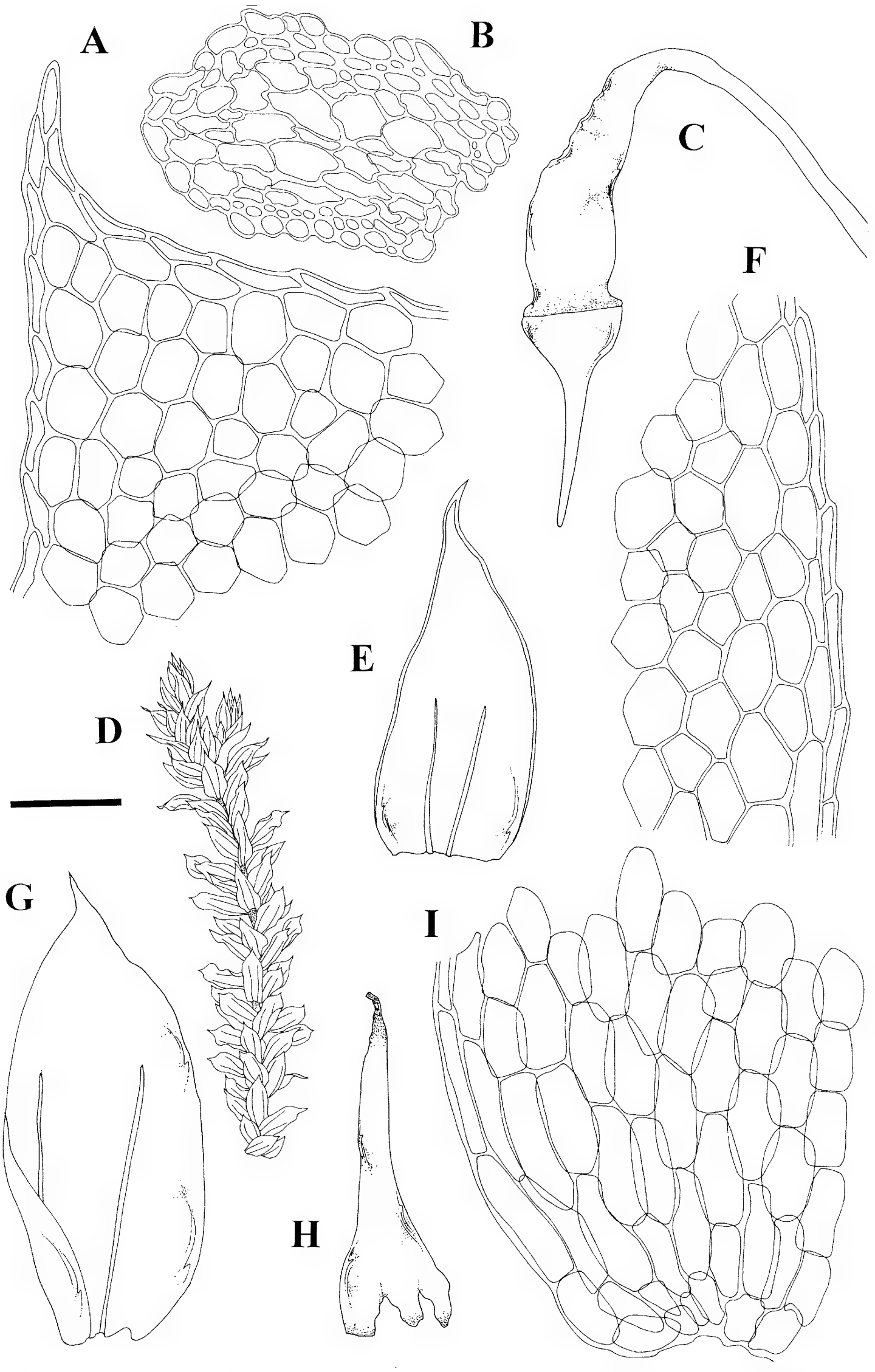
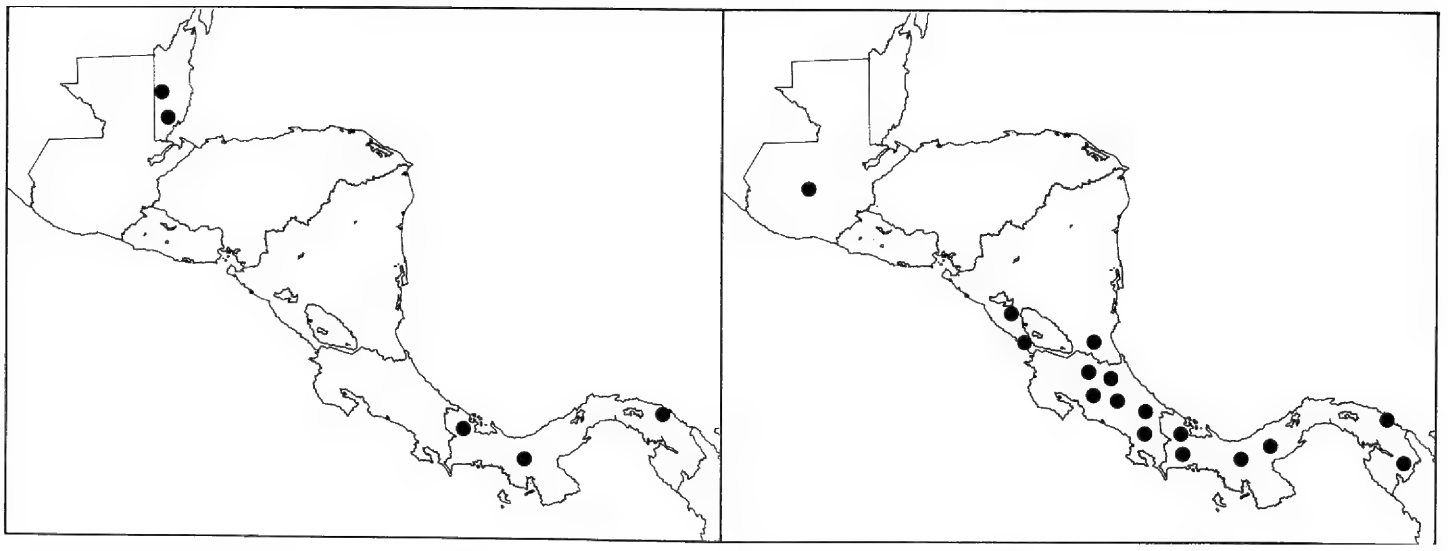


Figure 175. *Cyclodictyon varians*. A. Leaf apex. B. Stem in cross section. C. Seta, capsule, and operculum. D. Habit. E & G. Leaves. F. Median leaf cells and margin. H. Calyptra. I. Basal and alar cells. Scale in mm: bar = 0.06 (A, F, I); bar = 0.08 (B); bar = 0.28 (E, G); bar = 0.5 (C, H); bar = 1.96 (D). B from *Allen 18719*; C, H from *Wright 171*; all other figure parts from *Allen 5594*.



Cyclodictyon varians *Hemiragis aurea*

planate-foliate; stems in cross section with 1-stratose hyalodermis, subepidermis of 1–2 rows of smaller, thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia foliose; axillary hairs 2-cells long, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Lateral leaves not or weakly contorted, erect-spreading when dry, wide-spreading when wet, asymmetric, ovate to oblong-lanceolate, 1–2 mm long, gradually acuminate, shortly apiculate, concave; margins subentire to serrulate, broadly inflexed below on one side; obsoletely bordered by 1 row of narrow, elongate cells, confluent at the apices, plane; costae double, ending 2/3 the leaf length, diverging throughout, occasionally projecting at the apices, dorsal surface smooth; cells smooth, upper cells broadly hexagonal, 24–50 × 22–34 µm, laxly bulging, median and lower cells oblong-rectangular to long-rectangular; alar cells undifferentiated. Ventral and dorsal leaves symmetric, ovate, gradually acuminate. Asexual reproduction absent. Autoicous. Perigonia and perichaetia sessile along stems and branches. Setae elongate, 10–15 mm long, red to red brown, smooth. Capsules inclined to pendent, short-cylindric, neck moderately developed, 1–2 mm long; exothecial cells at mouth reddish, quadrate to shortly oblate in 2–3 rows, those below short-rectangular, lightly collenchymatous; stomata 4-celled, rudimentary, on neck; opercula long-rostrate, 1.0–1.2 mm long; annuli rudimentary, deciduous; peristome diplolepideous; exostome teeth narrowly triangular, with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface dark red, densely and closely striate below, coarsely papillose above, primary walls yellow, smooth, ventral (inner) surface hyaline to yellowish, deposition thin, lightly papillose, median lines weak; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, keeled, not or faintly perforate, cilia absent. Spores rounded to oval, 10–12 µm, faintly papillose. Calyptrae mitrate, yellowish white, irregularly lobed at base, naked, smooth, 1.5 mm long.

Illustrations. Grout (1934, Pl. 58 C); Welch (1962, Figs. 24–32); Breen (1963, Pl. 103 1–4); Crum and Anderson (1981, Fig. 395); Reese (1984, Fig. 44 F & G); Duarte Bello (1997, Pl. 239, as *C. cuspidatum*); Buck (1998, Pl. 9 1–3); Vaz and Costa (2006a, Figs. 85–89). Figure 175.

Habitat. On rocks, boulders or travertine, submerged in or along streams, and at the base of trees; 350–850 m.

Distribution in Central America. BELIZE. Cayo: *Allen 18318* (MO); Toledo: *Allen 18719* (MO). PANAMA. Bocas del Toro: *Allen 5594* (MO); San Blas: *D'Arcy 13632* (MO); Veraguas: *Crosby 10119* (MO).

World range: Southeastern U.S.A.; Mexico; Central America; Caribbean; Western and Northern South America.

Cyclodictyon varians is very much like *C. albicans* or *C. bicolor* in size, leaf shape, and color. It belongs to the *Cyclodictyon* group with enlarged, thin-walled, more or less hexagonal upper leaf cells

that also includes *C. crosbyi* and *C. fendleri*. The leaves of *C. varians* are bordered by a single row of elongate cells, and this is the outstanding distinguishing feature of the species. In addition, the leaf border varies from subentire to irregularly serrulate, and is never serrate. *Cyclodictyon albicans*, *C. crosbyi*, and *C. fendleri* differ fundamentally from *C. varians* in having stronger leaf borders that have 2–3 rows of elongate cells. *Cyclodictyon albicans* further differs in having strongly serrate leaves, while the leaves of *C. fendleri* differ from those of *C. varians* in ending in long, narrow acumina or hair-points. *Cyclodictyon crosbyi* is not likely to be confused with *C. varians* because of its smaller plant size and the presence of gemmae on the lower dorsal surface of the costae.

Cyclodictyon bicolor can often be distinguished from *C. varians* by its stronger leaf border, but the border in *C. bicolor* varies from one to two rows of elongate cells and this sometimes results in collections that are difficult to place. Moreover, the *albicaule*-form of *C. bicolor* has very weakly differentiated leaf borders, and at times its leaf margins are almost entirely one cell wide. In evaluating these difficult collections it is important to examine the border near the leaf apex. *Cyclodictyon bicolor* will have at least one place in which the leaf border is two cells wide, while the leaf borders in *C. varians* are more or less obsolete and never more than one cell wide.

7. *Hemiragis* (Brid.) Besch., Ann. Sci. Nat., Bot. sér. 6, 3: 1876. *Leskea* Hedw. subgen. *Hemiragis* Brid., Bryol. Univ. 2: 334. 1827. *Hookeria* Sm. sect. *Hemiragis* (Brid.) Mitt., J. Linn. Soc., Bot. 12: 335. 1869.

Plants medium-sized to robust, green, yellow, or yellowish red, in glossy, dense mats. Stems prostrate or suberect, irregularly, at times densely, branched; stems in cross section with 1-stratose hyalodermis, epidermis of smaller, thick-walled cells, enlarged, thin-walled cortical cells, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect, erect-twisted, erect-spreading to falcate when dry, little changed when wet, narrowly triangular, subulate-acuminate, deeply plicate, rounded to the insertions, decurrent by 1–2 enlarged, inflated cells; margins serrate to serrulate throughout, plane to erect, sometimes slightly recurved above; costae double, slender, more or less parallel throughout, 3/4–7/8 the leaf length, ending in projecting spines, at times toothed on dorsal surface; cells smooth, upper and median cells linear, straight to subflexuose, thick-walled, usually porose; basal cells across the insertions enlarged, rectangular, strongly porose, yellowish to reddish; alar cells undifferentiated. Asexual reproductive structures not seen. Autoicous. Setae elongate, flexuose, slightly roughened below the capsule, otherwise smooth. Capsules suberect to inclined, ovoid to ovoid-cylindrical, neck well developed; exothecial cells weakly collenchymatous; stomata rudimentary; opercula conic-rostrate, annuli rudimentary, deciduous; peristome diplolepideous; exostome teeth narrowly triangular, dorsal (outer) surface furrowed, densely cross-striate and papillose at base, papillose above, ventral (inner) surface as broad as the dorsal surface, lightly papillose; endostome as long as the exostome, basal membranes high, segments broad, deeply keeled, lightly perforate, cilia absent or rudimentary. Calyptrae mitrate, irregularly lobed at base, naked or sparsely hairy.

Hemiragis is a monospecific genus found only in the Caribbean, Central America, and northern South America. It usually has robust plants and sometimes grows in the canopy of trees. The plants have a glossy, green to yellowish or bronze color, and suberect, evenly foliate stems with a well-developed hyalodermis. The narrowly triangular leaves are deeply plicate, rounded to the insertions, and have serrate to serrulate, elimbate margins. Its leaf cells are linear, thick-walled, and usually porose, while the long, slender, double costae end in a projecting spine. The *Hemiragis* sporophytes have long, flexuose setae that are roughened above and ovoid to subcylindrical capsules with weakly collenchymatous exothecial cells. The exostome teeth are furrowed and densely cross-striate at base. The calyptrae are mitrate and lobed at base. As noted by Crosby and Allen (1985), some members of *Brymela* closely approach *Hemiragis* in their size and non-complanate habit. They are also similar in having leaves that are plicate at base, are rounded at the insertions, and have incrassate, porose cells. Furthermore, both genera have identical sporophytes and calyptrae. *Brymela* differs from *Hemiragis* in having a stem sclerodermis rather than a hyalodermis and oblong, oblong-lanceolate, or ovate-lanceolate leaves with better-developed costae. In those species of *Brymela* with leaves plicate at

base, the plicae are never as deep as the plicate leaves of *Hemiragis*. In this respect, the difference between the two genera is similar to the plicae difference between *Pireella* and *Pterobryon*.

The name *Hemiragis* apparently combines the Greek *hemi* (half) and *rhagas* (rent or torn). The meaning of the name is unclear; it might refer to the irregularly lobed, mitrate calyptrae of the genus, but this seems unlikely since Bridel did not see the calyptra.

Hemiragis aurea (Lam. *ex* Brid.) Kindb., Enum. Bryin. Exot. 16. 1888. *Hypnum aureum* Lam. *ex* Brid., Muscol. Recent. 2: 146. 1801. *Mnium aureum* (Lam. *ex* Brid.) P. Beauv., Prodr. Aethéogam. 74. 1805. *Harpophyllum aureum* (Lam. *ex* Brid.) Spruce, Cat. Musc. 11. 1867, combination invalid, genus illegitimate. *Hookeria aurea* (Lam. *ex* Brid.) Mitt., J. Linn. Soc., Bot. 12: 348. 1869. Protologue. In Antillis, unde clar. *La Mark.* accepit.

Leskea striata Schwägr., Sp. Musc. Frond. Suppl. 1(2): 180. 1816. *Hypnum phryxophyllum* Arn., Mém. Soc. Linn. Paris 5: 311. 1826, new name, not *Hypnum striatum* Schreb. *ex* Hedw., 1801. *Hookeria striata* (Schwägr.) Hampe, Linnaea 25: 363. 1853. *Hemiragis striata* (Schwägr.) Besch., Ann. Sci. Nat., Bot. sér. 6, 3: 242. 1876. Protologue. In monte sulphurifero Guadelupae legit et denominavit clar. *Richard.*

Hemiragis friedrichsthaliana Reichardt, Sitzungsber. Kaiserl. Akad. Wiss. Math.-Naturwiss. Cl., Abt. 1, 75: 579. 1877. Protologue. Quatemala [sic]; l. *Friedrichsthal.* Type. Guatemala. *Friedrichsthal*, 1841 (NY, isotype).

Plants medium-sized to robust, 3–12 cm long, green, yellow, or bronze, in glossy dense mats. Stems prostrate or suberect, sparsely to irregularly pinnately branched, red; stems in cross section with 1-stratose hyalodermis, epidermis of 3–5 rows of smaller, thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs fugacious, 2 cells long, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids not commonly encountered, on branches and stems in contact with substrate, from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect, erect-twisted, erect-spreading to falcate when dry, little changed when wet, narrowly triangular, 3–5 mm long, subulate-acuminate, deeply plicate, rounded to the insertions, decurrent by 1–2 enlarged, inflated cells; margins serrate to serrulate throughout, plane to erect, sometimes slightly recurved above; costae double, slender, more or less parallel throughout, 3/4–7/8 the leaf length, ending in a projecting spine, at times weakly toothed on dorsal surface; cells smooth, upper and median cells linear, straight to subflexuose, 40–80 × 4 µm, thick-walled, usually porose; basal cells across the insertions enlarged, rectangular, strongly porose, yellowish to reddish; alar cells undifferentiated. Asexual reproductive structures not seen. Autoicous. Perigonia and perichaetia enlarged and conspicuous, sessile along stems and branches. Setae elongate, flexuose, 30–45 mm long, red to red brown, slightly roughened below the capsule, otherwise smooth. Capsules suberect to inclined, ovoid to ovoid-cylindrical, 2.0–2.5 mm long, neck well developed; exothecial cells at mouth reddish, quadrate to shortly oblate, yellowish, in 2–3 rows, long-rectangular below, thick-walled, weakly collenchymatous; stomata rudimentary, on neck; opercula conic-rostrate, 1–2 mm long; annuli rudimentary, deciduous; peristome diplolepideous; exostome teeth erect to recurved when wet, incurved when dry, narrowly triangular, dorsal (outer) surface light yellow when young, becoming dark red with age, densely cross-striate and papillose at base, papillose above, ventral (inner) surface hyaline to yellowish, as broad as the dorsal surface, lightly papillose, dorsal trabeculae well developed, furrowed, ventral trabeculae moderately developed; endostome as long as the exostome, hyaline to yellowish, lightly papillose throughout, basal membranes high, segments broad, deeply keeled, narrowly perforate, cilia absent or rudimentary. Spores rounded to oval, 16–28 µm, faintly papillose. Calyptrae mitrate, red, roughened above, yellowish, smooth below, irregularly lobed at base, lobes rugose, naked or sparsely hairy, 2–3 mm long.

Illustrations. Bartram (1949, Fig. 144 A & B); Sharp *et al.* (1994, Fig. 622); Churchill and Linares (1995, Fig. 39 e–h); Buck (1998, Pl. 19 1–6); Gradstein *et al.* (2001, Fig. 167 A–E). Figure 176.

Habitat. On tree trunks, branches, twigs, and roots, at times in canopy, vines, logs, pendent on aerial roots, moist road banks, and wet rocks; 300–2500 m.

Distribution in Central America. GUATEMALA. Without locality, *Friedrichsthal* (NY). NICARAGUA. Granada: *Stevens 10867* (HNMN, MO); Río San Juan: *Shimek & Smith* (F); Rivas:

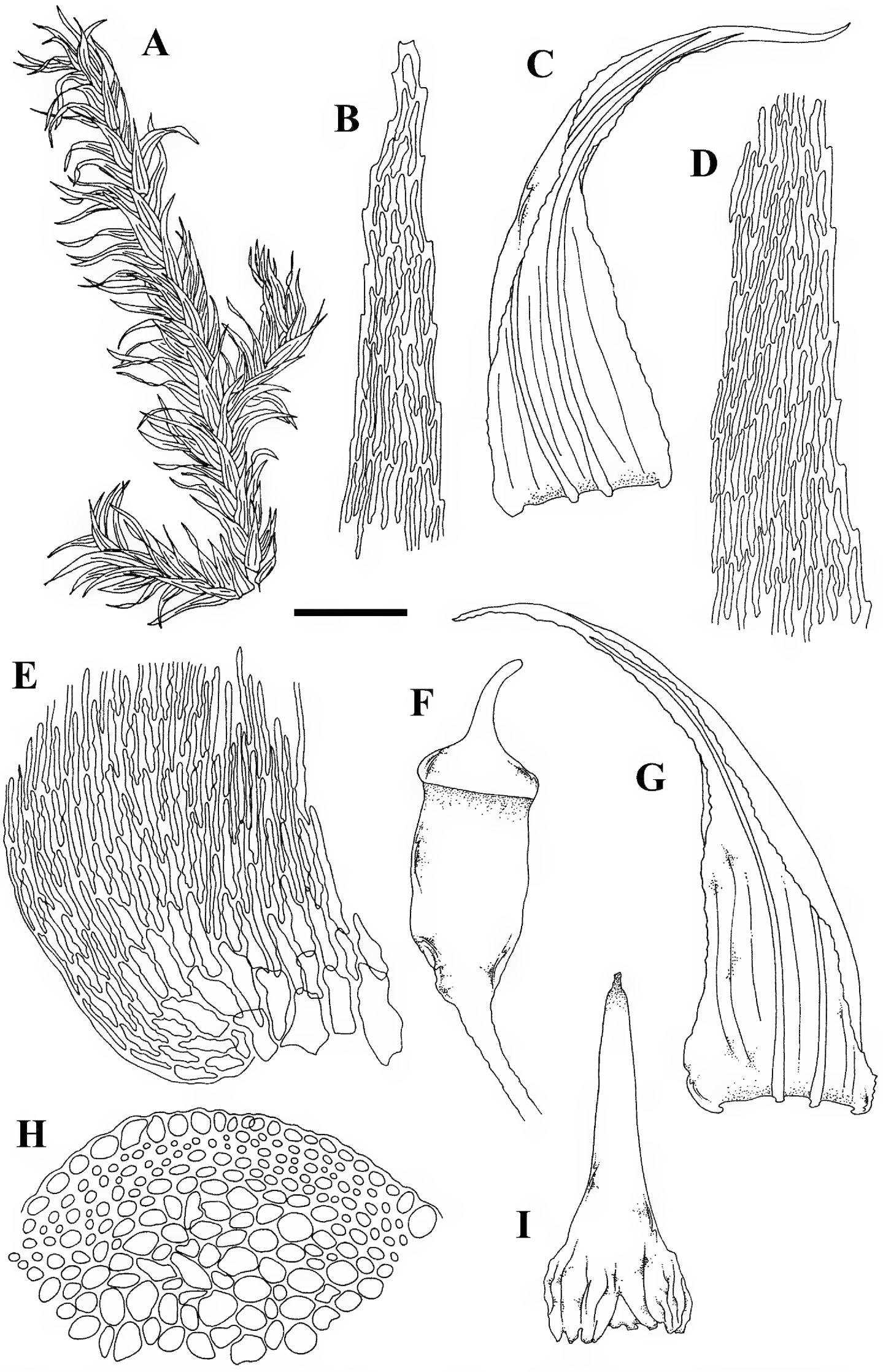


Figure 176. *Hemiragis aurea*. A. Habit. B. Leaf apex. C & G. Leaves. D. Median leaf cells and margin. E. Basal and alar cells. F. Seta, capsule, and operculum. H. Stem in cross section. I. Calyptra. Scale in mm: bar = 0.06 (B, D, E); bar = 0.13 (H); bar = 0.71 (C, G); bar = 0.9 (F, I); bar = 4.0 (A). F from *McPherson 8589*; I from *Lyon 45*; H from *Crosby 9994*; all other figure parts from *Allen 5095A*.

Moreno 19781 (MO, NY). COSTA RICA. Alajuela: *Liesner et al. 15632* (FH, MO); Cartago: *Griffin et al. 193* (F, MO, NY); Heredia: *Valerio 357* (FH); Limón: *Gómez & Herrera 23461* (MO, NY, US); Puntarenas: *Lyon 156* (FH, MO); San José: *Crosby 13135* (MO). PANAMA. Bocas del Toro: *Allen 5095A* (MO); Chiriquí: *McPherson 7780A* (MO); Coclé: *Tyson 2472F* (MO, NY); Darién: *Folsom 4390* (MO); San Blas: *Sytsma et al. 2703* (MO, PMA); Veraguas: *Mori & Kallunki 5366* (MO, PMA).

World range: Central America; Caribbean; Western and Northern South America.

Hemiragis aurea is a medium-sized to robust species that grows in dense, glossy mats. Its plants vary from green to bronze and are sometimes found on upper tree branches or in the tree canopy. The stems have a well-developed hyalodermis and no central strand. The plants are more or less stiffly suberect, and as a result rhizoids can be difficult to find since they appear to occur only when the stems or branches are in contact with the substrate. In Caribbean material of *H. aurea*, the stems have foliose pseudoparaphyllia (Buck 1998), but in Central American plants, the branch primordia are naked. The leaves of *H. aurea* are narrowly triangular and deeply plicate. Its double costae are long and slender, with each fork ending in a projecting spine. Occasionally, the dorsal surfaces of the costae are weakly toothed. The leaf cells are linear throughout, except at the very base where they become broadly rectangular, thick-walled, and usually porose. The alar cells are undifferentiated. The setae of *H. aurea* are remarkably long, flexuose, and roughened below the ovoid to subcylindrical capsules. Its exothecial cells are weakly collenchymatous, and the numerous stomata are rudimentary in form. The exostome teeth are furrowed and densely cross-striate at base. The endostomial segments are deeply keeled and have well-developed transverse walls on the inner surface that have been described as "baffle-like crosswalls" (Buck 1998). The calyptrae are mitrate and have irregular, rugose basal lobes.

Palamocladium and some species of *Breutelia* can be confused with *Hemiragis aurea* in the field, because their plants have the same size and color, and both genera have species with narrowly triangular, deeply plicate leaves. Plants of *Palamocladium* and *Breutelia*, though, are usually densely tomentose, and this can be used to separate them in the field from *H. aurea*. Under the microscope, the presence of leaves with long, single costae in both *Palamocladium* and *Breutelia* distinguishes them from *H. aurea.* There are some species of *Brymela* and *Thamniopsis* that approach *H. aurea* in size, and all three genera share many technical gametophytic and sporophytic features. However, these genera never have narrowly triangular leaves that are as strongly plicate as those of *H. aurea*. *Brymela* further differs from *H. aurea* in lacking a stem hyalodermis, while *Thamniopsis* species have enlarged, thin-walled basal leaf cells.

Hemiragis aurea is fairly common in the cloud forests of Panama and Costa Rica, as well as lowland areas of Costa Rica and southernmost Nicaragua. There is one historical collection of the species from Guatemala, and Crum (1994b) thought the species might be found in Mexico. However, *H. aurea* is unlikely to be overlooked in the field due to its large size and occurrence in dense mats. Since Mexico, Belize, and Honduras have been extensively collected, it seems possible it may not occur there. The Caribbean distribution of *H. aurea* is also uneven: common in the Lesser Antilles and Puerto Rico; rare in Hispaniola and Jamaica; absent in Cuba.

8. *Hookeria* Sm., Trans. Linn. Soc. London 9: 275. [1 Jun] 1808 , conserved name, not *Hookeria* Salisb., [1 Mar] 1808.

Plants medium-sized to robust, pale green or yellowish green, lustrous, in thin mats. Stems prostrate, simple or sparsely and irregularly branched, hyaline to yellowish when young, becoming reddish with age, complanate-foliate; stems in cross section with epidermis and cortical cells enlarged, thin-walled, central strand rudimentary to weakly developed; paraphyllia absent; pseudoparaphyllia foliose; axillary hairs 2–3 cells long, basal cell quadrate, hyaline, median cell (when present) subrectangular, hyaline, upper cell oblong, reddish brown; rhizoids from initials abaxial to the leaf insertions, reddish brown, not or sparsely and irregularly branched. Leaves not or slightly contorted when dry. Lateral leaves flattened, wide-spreading when wet, slightly asymmetric; margins entire, not or obscurely bordered by a single row of somewhat elongate and broader cells, plane; costa absent, or leaves with bistratose region at the very base; cells smooth, elongate-hexagonal to rhomboidal, laxly bulging; alar cells undifferentiated. Dorsal leaves erect, symmetric, ovate to oblong-ovate, acute or obtuse; margins plane. Asexual reproduction by reddish brown, papillose-roughened, rhizoid-like

propagula, usually with straight cross-walls originating from nematogen cells at leaf apices and along or near leaf margins. Autoicous. Perigonia and perichaetia sessile along stems and branches. Setae elongate, reddish to orange, smooth, flexuose. Capsules inclined to pendent, ovoid to short-cylindric, neck moderately developed; exothecial cells collenchymatous; stomata on neck; opercula conic to conic-rostrate; annuli rudimentary, deciduous; peristome diplolepideous; exostome teeth narrowly triangular, dark red, not furrowed, densely and closely cross-striate below, coarsely papillose above, median line and trabeculae weakly developed, ventral surface smooth, trabeculae well developed and projecting; endostome as long as the exostome, yellowish white, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, faintly perforate, cilia absent. Calyptrae mitrate, yellowish white, irregularly lobed at base, naked, fleshy, 3–5 cells thick, inner 2 layers small, thick-walled, reddish, outer 3 layers enlarged, thin-walled, hyaline.

Hookeria is a genus of nine species (Crosby *et al.* 2000), only two of which have been critically studied. The most common and well-known species, *H. acutifolia*, is found throughout the world. *Hookeria magellanica* (P. Beauv.) Arn. (Type. l'herbier de M. de Jussieu, détroit de Magellan [Chile or Argentina]), however, may be the same, and it predates *H. acutifolia* by 20 years. *Hookeria* is a genus of medium-sized to large plants that have a soft, pale green color and strongly complanate-foliate stems. Unlike most other members of the Hookeriaceae, the stem of *Hookeria* has a rudimentary or weakly developed central strand. The leaves are mostly ovate and ecostate, and they have extremely large, thin-walled leaf cells. Sporophytically, the genus has inclined to pendent capsules, with exostome teeth densely cross-striate on the dorsal surface and no median furrows. The endostome is typical for the Hookeriaceae: high basal membranes, stout, strongly keeled, weakly perforate segments, and no cilia. *Hookeria* has unusually fleshy calyptrae that consist of 3–5 cell layers, with the outer 2–3 layers made up of enlarged, thin-walled, and hyaline cells.

Buck (1987, 1998) reduced the Hookeriaceae to include only *Achrophyllum* Vitt & Crosby, *Cyathophorella* (Broth.) M. Fleisch., *Cyathophorum* P. Beauv., *Dendrocyathophorum* Dixon, *Hookeria*, and *Schimperobryum* Margad. All members of this group (except *Schimperobryum* and *Hookeria*) have single costae, but Buck (1987) considered the group unified by the presence of stem central strands, undifferentiated stem cortices, and thick-walled calyptrae. Whittemore and Allen (1989) considered the group unified only by the presence of a stem central strand, and, since they considered the presence of a central strand to be a primitive feature of the group, returned *Hookeria* to the bicostate/ecostate cluster of genera. A molecular study of the Hookeriales (Buck *et al.* 2005) restricted the Hookeriaceae to *Hookeria* and possibly *Crossomitrium*. These genera have ecostate leaves, but they otherwise have very little in common except generalized Hookeriaceae features.

The name *Hookeria* honors Sir William Jackson Hooker (1785–1865), British botanist and director of the Royal Botanic Gardens, Kew, 1841–1865. Hooker was the author of *Musci exotici* and coauthored (with Thomas Taylor) *Muscologia britanica*. An indication of the importance of W. J. Hooker to botany is evident from his entry in *Taxonomic Literature–2* (Stafleu & Cowan 1979), which runs to 19 pages. Joseph Dalton Hooker was one of his sons.

Hookeria acutifolia Hook. & Grev., Edinburgh J. Sci. 2: 225. 1825. *Pterygophyllum acutifolium* (Hook. & Grev.) Müll. Hal., Linnaea 21: 194. 1848. Protologue. [Nepal] Hab. Nepaul, *Dr. Wallich.*

Plants medium-sized to robust, 3–8 cm long, pale green or yellowish green, lustrous, in thin mats. Stems prostrate, simple or sparsely and irregularly branched, hyaline to yellowish when young, becoming reddish with age, complanate-foliate; stems in cross section with epidermis and cortical cells enlarged, thin-walled, central strand rudimentary to weakly developed; paraphyllia absent; pseudoparaphyllia foliose; axillary hairs fugacious, 2–3 cells long, basal cell quadrate, hyaline, median cell (when present) subrectangular, hyaline, upper cell oblong, reddish brown; rhizoids from initials abaxial to the leaf insertions, reddish brown, papillose-roughened, not or sparsely and irregularly branched. Leaves not or slightly contorted when dry. Lateral leaves flattened, wide-spreading when wet, slightly asymmetric, ovate to oblong-ovate, 3–6 mm long, gradually acute to bluntly acute, sometimes rounded; margins entire, plane, not or obscurely bordered by a single row of somewhat elongate and broader cells; costa absent, or leaves with bistratose region at the very base; cells smooth, elongate-hexagonal to rhomboidal, 102–205 × 41–62 μm, laxly bulging; alar cells undif-

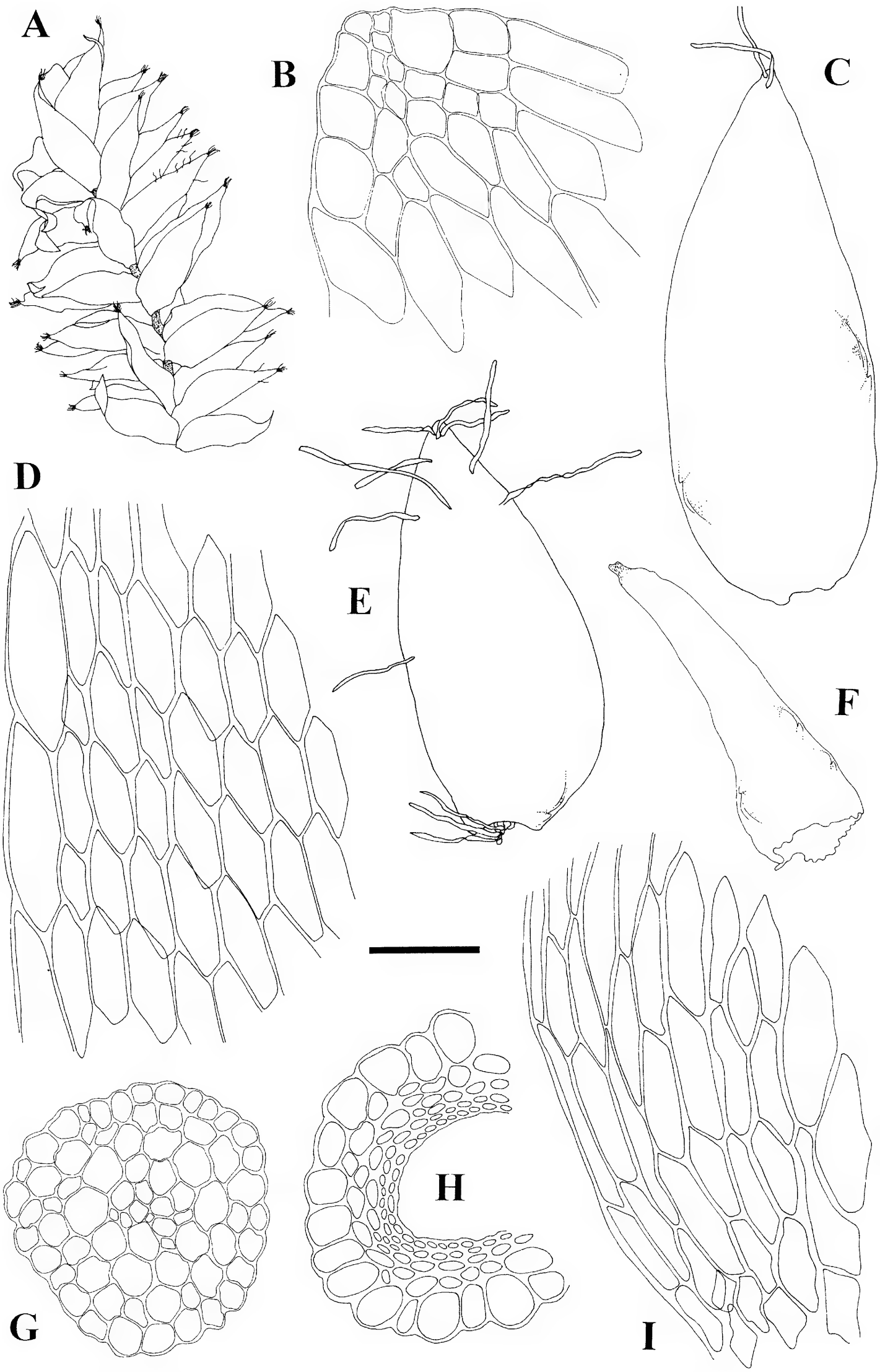
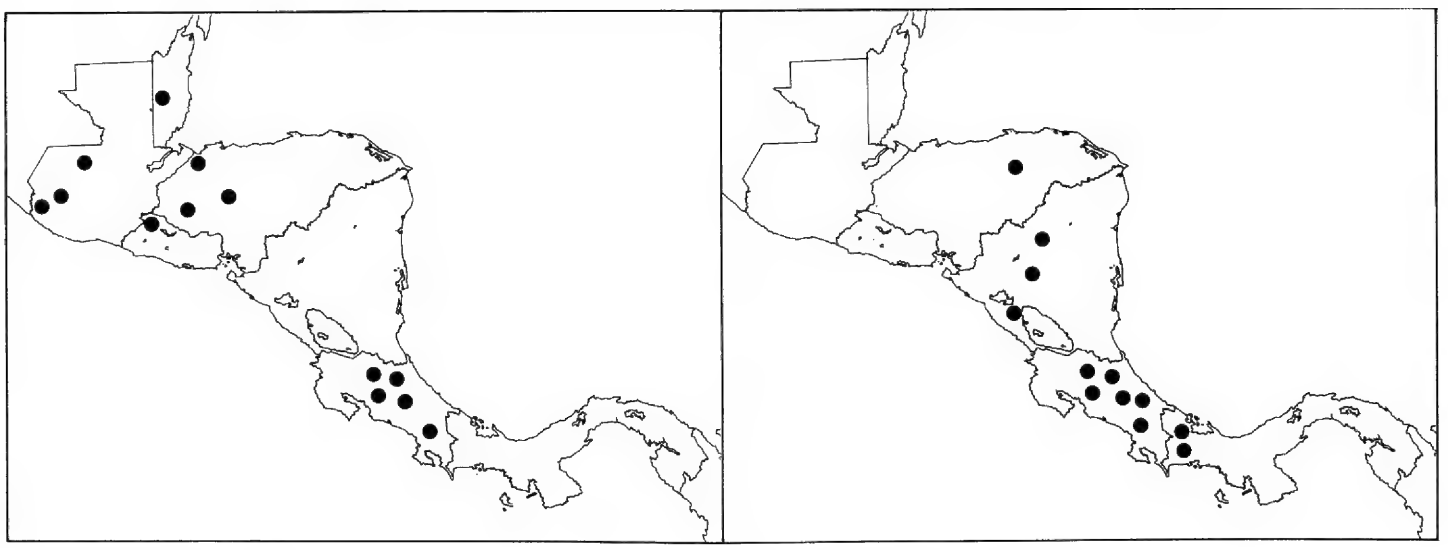


Figure 177. *Hookeria acutifolia*. A. Habit. B. Leaf apex. C & E. Leaves. D. Median leaf cells and margin. F. Calyptra. G. Stem in cross section. H. Calyptra in cross section. I. Basal and alar cells. Scale in mm: bar = 0.08 (B); bar = 0.13 (D, I); bar = 0.17 (G, H); bar = 0.5 (C, E); bar = 0.6 (F); bar = 4.0 (A). B from *Liesner 14503*; F, H from *Crosby 9712*; all other figure parts from *Allen 14093*.



Hookeria acutifolia *Hypnella diversifolia*

ferentiated. Dorsal leaves erect, symmetric; margins plane. Asexual reproduction by reddish brown, papillose-roughened, rhizoid-like propagula, usually with straight cross-walls originating from nematogen cells at leaf apices and along or near leaf margins. Autoicous. Perigonia and perichaetia sessile along stems and branches. Setae elongate, 8–20 mm long, reddish to orange, smooth, flexuose. Capsules inclined to pendent, ovoid to short-cylindric, neck moderately developed, 1–2 mm long; exothecial cells at mouth reddish, quadrate to shortly oblate in 5–8 rows, short-rectangular below, collenchymatous; stomata on neck; opercula conic to conic-rostrate, 0.7–1.0 mm long; annuli rudimentary, deciduous; peristome diplolepideous; exostome teeth narrowly triangular, dark red, not furrowed, densely and closely cross-striate below, coarsely papillose above, median line and trabeculae weakly developed, ventral surface smooth, trabeculae well developed and projecting; endostome as long as the exostome, yellowish white, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, faintly perforate, cilia absent. Spores rounded, 12–16 µm, faintly papillose. Calyptrae mitrate, yellowish white, irregularly lobed at base, naked, fleshy, 3–5 cells thick, inner 2 layers small, thick-walled, reddish, outer 3 layers enlarged, thin-walled, hyaline, 1.5–2.0 mm long.

Illustrations. Hooker and Greville (1825, Pl. 5); Schwägrichen (1826, Pl. 163 1); Britton (1894, Pl. 80, as *Hookeria sullivantii*); Fleischer (1908, Fig. 172); Bartram (1933a, Fig. 143); Grout (1934, Pl. 58 B); Bartram (1949, Fig. 133 A–C); Jennings (1951, Pl. 67); Welch (1962, Figs. 8–15); Lawton (1971, Pl. 134 15–18, Pl. 135 1–5); Gangulee (1977, Fig. 747); Crum and Anderson (1981, Fig. 394); Noguchi (1991, Fig. 331); Sharp *et al.* (1994, Fig. 582); Churchill and Linares (1995, Fig. 102 a–d); Lin and Tan (1995, Fig. 36); Duarte Bello (1997, Pl. 243); Buck (1998, Pl. 5 1–4); Gradstein *et al.* (2001, Fig. 134 L–P). Figure 177.

Habitat. On soil, sand, or rocks along stream or trail banks, occasionally on wet logs and tree bases near streams or in very wet forests, also at base of vertical rock faces; 1500–3130 m.

Distribution in Central America. BELIZE. Cayo: *Allen 15137* (MO). GUATEMALA. Quetzaltenango: *Standley 65338* (F, FH); Quiché: *Sharp 2513* (FH); San Marcos: *Steyermark 36400* (F, FH, US). EL SALVADOR. Santa Ana: *Davidse et al. 37207* (MO). HONDURAS. Comayagua: *Allen 13965* (MO); Cortés: *Allen 14091* (MO); Lempira: *Allen 11479* (MO). COSTA RICA. Alajuela: *Crosby 9974* (MO); Cartago: *Dauphin & Ramírez 2061* (MO); Heredia: *Crosby & Crosby 6048* (FH, MO); Puntarenas: *Lyon 454* (MO); San José: *Crosby & Crosby 5773* (MO).

World range: Western Canada; Northeastern, Southeastern, North-Central, and Northwestern U.S.A.; Mexico; Central America; Caribbean; Western and Northern South America, Brazil; Caucasus, China, Eastern Asia; Indian Subcontinent, Indo-China, Malesia; North-Central Pacific.

Hookeria acutifolia is a beautiful, large species that can be immediately recognized in the field by its pale green color, complanate-foliate stems, large, soft leaves, and exceptionally big, lax leaf

cells. Indeed the cells are so large that, as noted by Crum and Anderson (1981) and Buck (1998), they can easily be seen with a hand lens. The stems have a small cluster of rhizoidal initials positioned abaxially to the leaf insertions and papillose-roughened rhizoids. Unlike most other members of the Hookeriaceae, the stems have central strands that vary from rudimentary to weakly but distinctly present. Nearly all collections have numerous leaves with odd rhizoid-like propagula at the apices and scattered near the leaf margins. When young these structures are short, have straight cross-walls, and seem clearly to be propagula. However, as they age they become elongate, have somewhat oblique walls, and look more rhizoid-like. Although the leaves are typically acute, those with apical propagula are commonly broadly rounded. Distinctive microscopic features of the leaves include the absence of a costa; regularly elongate-hexagonal to rhomboidal, very wide, smooth cells; and marginal cells that are usually longer and broader than the interior cells, forming an obscure border. The exostome teeth of *H. acutifolia* are densely cross-striate on the lower dorsal surface, with no hint of median furrows. The endostome is typical for the Hookeriaceae: high basal membranes, stout, strongly keeled, weakly perforate segments, and no cilia.

9. *Hypnella* (Müll. Hal.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 365. 1877.
Hookeria Sm. sect. *Hypnella* Müll. Hal., Syn. Musc. Frond. 2: 208. 1851. *Hookeria* Sm. subgen. *Hypnella* (Müll. Hal.) Hampe, Verh. Zool.-Bot. Ges. Wien 21: 391. 1871.

Hookeria Sm. sect. *Hypnella* Müll. Hal. subsect. *Euhypnella* Müll. Hal., Syn. Musc. Frond. 2: 208. 1851.
Hylotapis Spruce, Cat. Musc. 10. 1867, invalid name, lacks a description.
Hookeria Sm. subsect. *Hylotapis* Spruce *ex* Mitt., J. Linn. Soc., Bot. 12: 338, 363. 1869.
Neohypnella E. B. Bartram, Contr. U.S. Natl. Herb. 26: 104. 1928.

Plants slender, medium-sized, or robust, in glaucous, dull or shiny, pale green, green, yellowish green, or yellowish red, occasionally purple tinged mats, sometimes pendent. Stems creeping, sparsely or densely, irregularly to subpinnately branched, weakly or not complanate-foliate; in cross section hyalodermis or sclerodermis present, subepidermal cells small, thick-walled, red brown, cortical cells enlarged, thin- or firm-walled, yellowish or hyaline, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell quadrate, red brown, upper cell enlarged, oblong, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves flattened, secund, erect, imbricate, weakly contorted when dry, erect, erect-spreading, or secund when wet, broadly ovate, ovate, elliptical-oblong, oblong-lanceolate, or lanceolate, concave, apices obtuse, acute, acuminate to filiform-acuminate, apices sometimes recurved; margins entire, serrulate, serrate, papillose-roughened, or denticulate, erect, recurved or reflexed, border absent or weak; costae double (ecostate in *H. guayanensis*), strong and ending below the apex or weak and ending below midleaf, at times ending as a spine or dorsal crest; cells rectangular to elongate-fusiform or vermicular, pluripapillose (sometimes smooth in *H. guayanensis*), papillae seriate, short or high, frequently branched, cells becoming shorter, wider, laxer, and more or less smooth toward the insertions; alar cells not differentiated. Autoicous, synoicous, or dioicous. Setae elongate, red, papillose to scabrous above (occasionally smooth). Capsules long-exserted, cylindrical to oblong, erect, inclined or pendent, neck often papillose or scabrose; exothecial cells often collenchymatous; stomata rudimentary; opercula conic-rostrate; annulus rudimentary; peristome diplolepideous, xerocastique (hydrocastique in *H. diversifolia*); exostome teeth reddish brown (hyaline in *H. diversifolia*), narrowly triangular, on dorsal (outer) surface usually densely cross-striate below, furrowed or not furrowed; endostome yellow, smooth or weakly papillose, basal membranes high, segments long, broad-keeled, more or less perforate, cilia absent or vestigial. Calyptrae mitrate, roughened above, irregularly lobed at base.

Hypnella is a Neotropical genus of seven species. Its leaves characteristically have long, well-developed, double costae; elongate, narrow, seriately pluripapillose leaf cells; and undifferentiated alar cells. Its sporophytes typically have collenchymatous exothecial cells and xerocastique peristomes, with exostome teeth that are densely cross-striate on the dorsal surface and strongly furrowed. However, one species (*H. guayanensis*) has leaves with either pluripapillose or smooth cells and it, along with *H. pallescens*, has weakly costate or ecostate leaves. In addition, *H. diversifolia* has

non-collenchymatous exothecial cells and hydrocastique peristomes, with weakly cross-striate, non-furrowed exostome teeth. These three odd species of *Hypnella* also differ significantly from the others in having a stem sclerodermis rather than a hyalodermis. The genus appears to be polyphyletic.

Hypnella diversifolia not only has an odd peristome, but, unlike the other species in the genus, it is primarily an epiphytic species that often grows on twigs and occasionally is epiphyllous. Bartram (1928a) established the genus *Neohypnella* for *H. diversifolia*, because it had zigzag median lines rather than median furrows on the dorsal surface of the exostome teeth. Since *Neohypnella* and *Hypnella* apparently differed only in the presence or absence of furrowed exostome teeth Crosby *et al.* (1985) synonymized the two taxa. However, there is molecular evidence indicating significant differences between *H. diversifolia* and *H. pallescens*, and this led Buck *et al.* (2005) to suggest *Neohypnella* should be recognized. In view of the many distinctive features of *H. diversifolia*, the genus *Neohypnella* should probably be resurrected.

Welch (1969) lectotypified *Hypnella* with *Hookeria pallescens*. In a review of the genus, however, Crosby *et al.* (1985) argued against that lectotypification and proposed to supersede her decision, designating *Hookeria leptorrhyncha* as the lectotype of the genus. The correct lectotypification of *Hypnella* takes on added importance because, as noted above, *H. pallescens* and *H. guayanensis* appear to be distinctly, perhaps at the generic level, different from *H. leptorrhyncha*.

Hypnella has been placed in the Sematophyllaceae (Crosby 1974b; Walther 1983; Vitt 1984; Crosby *et al.* 1985) because of its similarity to a group of genera (*Taxithelium*, *Glossadelphus*, and *Pseudohypnella*) with linear, seriately pluripapillose leaf cells, double costae, no stem central strand, and cross-striate exostome teeth. That group of genera, however, has a hypnaceous endostome (moderate-sized; membranous; segments medium-sized, strongly keeled and perforate; cilia well developed), while *Hypnella* has a hookeriaceous endostome (large; firm; segments broad, stout, keeled but not necessarily perforate; cilia absent or vestigial). Furthermore, the complete absence of alar cell development in *Hypnella* and its often very long, double costae indicate the genus is better placed in the Hookeriaceae. Crosby *et al.* (1985) reviewed *Hypnella*, examined most of the type specimens, and proposed most of the following synonymy.

The name *Hypnella* combines the generic name *Hypnum* with the Latin diminutive *-ella*.

1. Leaves long-acuminate 2
1. Leaves acute (occasionally short-acuminate), subacute, or obtuse 5

2. Leaves rounded to abruptly subpiliferous to piliferous apices 3
2. Leaves gradually and evenly long-acuminate to piliferous apices 4

3. Papillae short, more or less obscure; upper leaf margins serrate by projecting cell end walls; marginal cells mostly smooth; costae not or very weakly projecting at dorsal tips by a single cell; setae 10–15 mm long . . . . . [4. *H. leptorrhyncha*]
3. Papillae high (sometimes curved), prominent; upper leaf margins serrate to denticulate by lateral projecting papillae and projecting cell end walls; marginal cells in upper 1/2 pluripapillose; costae usually spined or crested at dorsal tips by 1–3 cells; setae 15–35 mm long . . . . . 6. *H. pilifera*

4. Marginal leaf cells long, narrowly fusiform; dorsal costal surface smooth, costae not or weakly projecting as a spine . . . . . [4. *H. leptorrhyncha*]
4. Marginal leaf cells short, broadly rectangular; upper dorsal costal surface serrate, costae strongly projecting by two or more cells at tip . . . . . [1. *H. ambrosia*]

5. Leaves ecostate; some leaves with cells entirely pluripapillose and others partly to entirely smooth . . . . . [3. *H. guayanensis*]
5. Leaves costate; all apical and median leaf cells pluripapillose 6

6. Leaves acute (occasionally short-acuminate); apical margins serrate by projecting cell end walls, obscurely bordered by long, narrow, more or less smooth cells . . . . . [7. *H. punctata*]
6. Leaves subacute or obtuse; apical margins serrate due to lateral, projecting papillae, not bordered 7

7. Plants usually glaucous, green; leaves rounded-obtuse, 0.5–1.0 mm long; most papillae stellate-branched; costae weak, 1/4–1/2 the leaf length; exostome teeth red, furrowed; capsule neck tuberculate . . . . . 5. *H. pallescens*
7. Plants usually glossy, golden red; leaves subacute, apiculate, apices often recurved, 0.9–1.4 mm long; papillae mostly simple; costae strong, 2/3–3/4 the leaf length; exostome teeth yellowish white, not furrowed; capsule neck smooth or papillose . . . . . 2. *H. diversifolia*

1. *Hypnella ambrosia* M. A. Lewis & B. H. Allen, Novon 2: 355. 1992. Protologue. Bolivia. Santa Cruz: Prov. Ichilo, Cerro Amboró, between upper Río Isama and summit, ca. 35 km S of Buena Vista, Parque Nacional de Amboró, 17°45′S, 63°39′W, ca. 900 m, *Lewis 37820*. Type. Bolivia. Santa Cruz: Prov. Ichilo, Cerro Amboró. Climb to the summit of Cerro Amboró from the upper part of the Rio Isama to the summit. Ca. 35 km S of Buena Vista, Parque Nacional de Amboró, 17°45′S, 63°39′W, ca. 900 m, *Lewis 37820* (MO, isotype).

Plants in thin, green mats, occasionally purple tinged, 2–3 cm long. Stems irregularly branched, red; stems in cross section with some enlarged epidermal cells forming a partial hyalodermis, otherwise cells small, thick-walled, red, cortical cells enlarged, firm-walled, yellowish to hyaline, central strand absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell quadrate, red brown, upper cells enlarged, oblong, hyaline; rhizoids not seen. Leaves flattened, erect when dry, spreading to wide-spreading when wet, lanceolate to oblong-lanceolate, gradually narrowed to long, slender, flexuose acumina, 1.0–1.8 × 0.15–0.30 mm; margins weakly serrate below, strongly serrate at apex, teeth mostly single, occasionally double, teeth often papillose-tipped, cells somewhat wider and shorter than laminal cells; costae double, long, ending in 1–2-celled spines, serrate along the upper dorsal surface; cells thin-walled, with 1–4 scattered papillae, at times papillae in horizontal rows, upper cells rectangular to elongate-fusiform to vermicular, 12–53 × 6–8 µm; basal cells long-rectangular, 25–47 × 5–6 µm, cells across the insertions reddish or hyaline, rectangular, 30–40 × 6–8 µm. Sporophytes unknown.

Illustrations. Lewis and Allen (1992, Figs. 1–7). Figure 178.
Habitat. On soil and bare stream banks in seepy area near springs and rills; 900–1250 m.
Not known from Central America.
World range: Western South America.

Hypnella ambrosia belongs to the piliferous-leaf group of *Hypnella* species (*H. ambrosia*, *H. leptorrhyncha*, *H. pilifer*). Indeed, its outstanding feature, visible using a hand lens, is the presence of leaves with very long, piliferous apices. *Hypnella ambrosia* is known only from the type locality in Bolivia, where it occupies a semi-aquatic habitat along streams and in seeps near springs. *Hypnella leptorrhyncha* is similar to *H. ambrosia* in having leaves that are gradually narrowed to the long piliferous apices, but the presence of costae that are serrate on the upper dorsal surface and strongly project at the tips by two or more, often pluripapillose, cells sets the species apart from all other members of *Hypnella.* Additionally, unlike the other members of the piliferous-leaf group, the marginal cells in *H. ambrosia* tend to be short and broadly rectangular. In *H. leptorrhyncha*, the costae are smooth on the upper dorsal surface, they do not or only weakly project at the tips by single cells, and the marginal cells are long and narrowly fusiform. The leaves of *H. pilifer* differ from those of *H. ambrosia* in their oblong shape and in being abruptly rounded to the acumen.

2. *Hypnella diversifolia* (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 366. 1877. *Hookeria diversifolia* Mitt., J. Linn. Soc., Bot. 12: 364. 1869. *Neohypnella diversifolia* (Mitt.) W. H. Welch & H. A. Crum, Bryologist 62: 174. 1960. Protologue. [Ecuador] Andes Quitenses, in sylva Canelos (3000 ped.), *Spruce, n. 678*. Type. Sylva de Canelos, And. Quitensis, 3000 ft. *Spruce 678* (FH, isotype).

Hookeria chrysophyllopodia Müll. Hal., Hedwigia 37: 249. 1898. *Hypnella chrysophyllopodia* (Müll. Hal.) Broth., Nat. Pflanzenfam. I(3): 950. 1907. *Neohypnella chrysophyllopodia* (Müll. Hal.) E. B. Bartram, Contr. U.S. Natl. Herb. 26: 104. 1928. Protologue. Insula Trinidad Antillarum, monte Tocuche, Junio 1847, sterilis: *Crüger*, qui misit 1848.

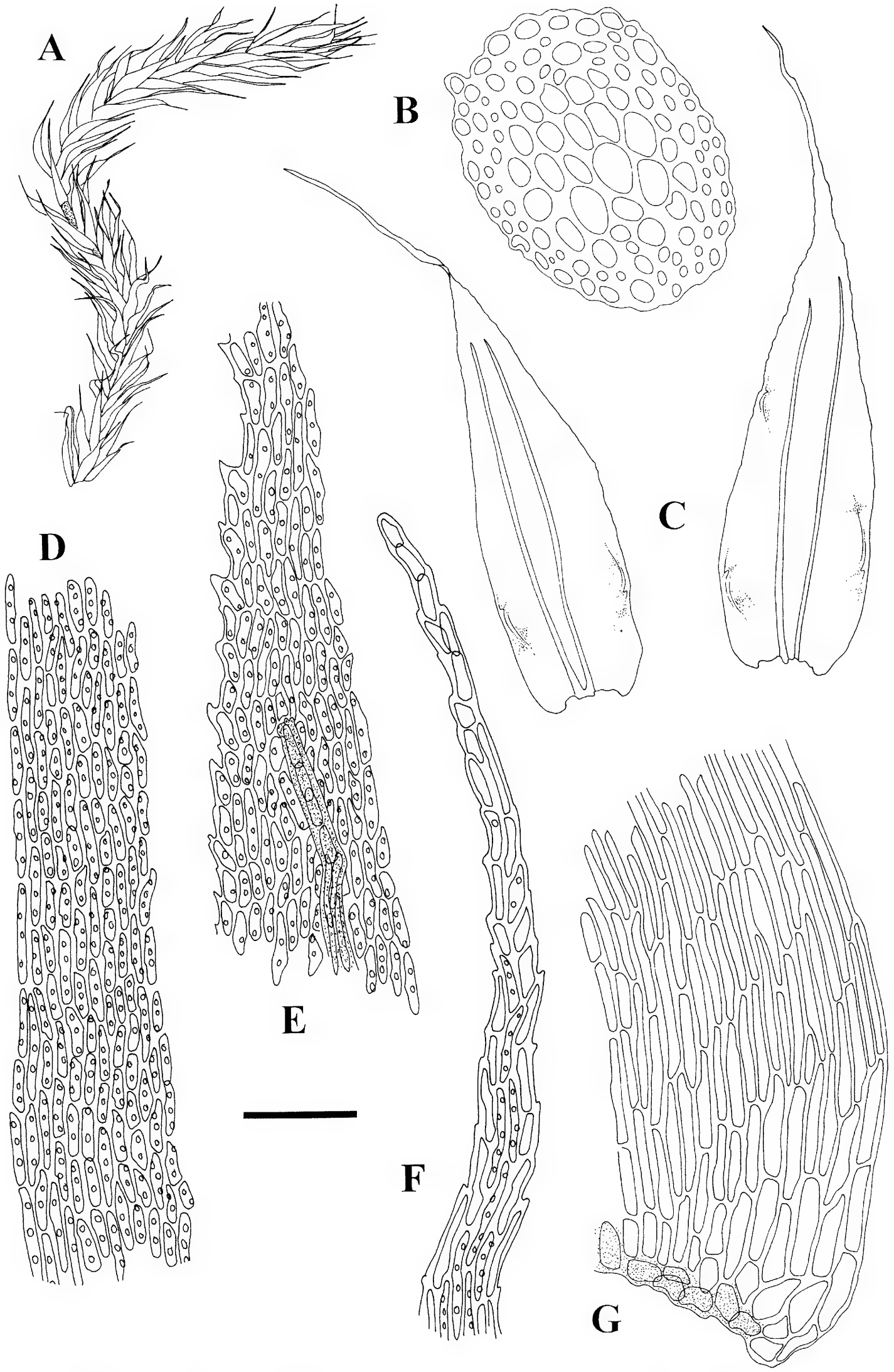


Figure 178. *Hypnella ambrosia*. A. Habit. B. Stem in cross section. C. Leaves. D. Median leaf cells. E. Upper leaf cells and margin. F. Leaf apex. G. Basal and alar cells. Scale in mm: bar = 0.04 (D–F); bar = 0.05 (G); bar = 0.06 (B); bar = 0.28 (C); bar = 1.56 (A). All figure parts from *Lewis 37820* (type).

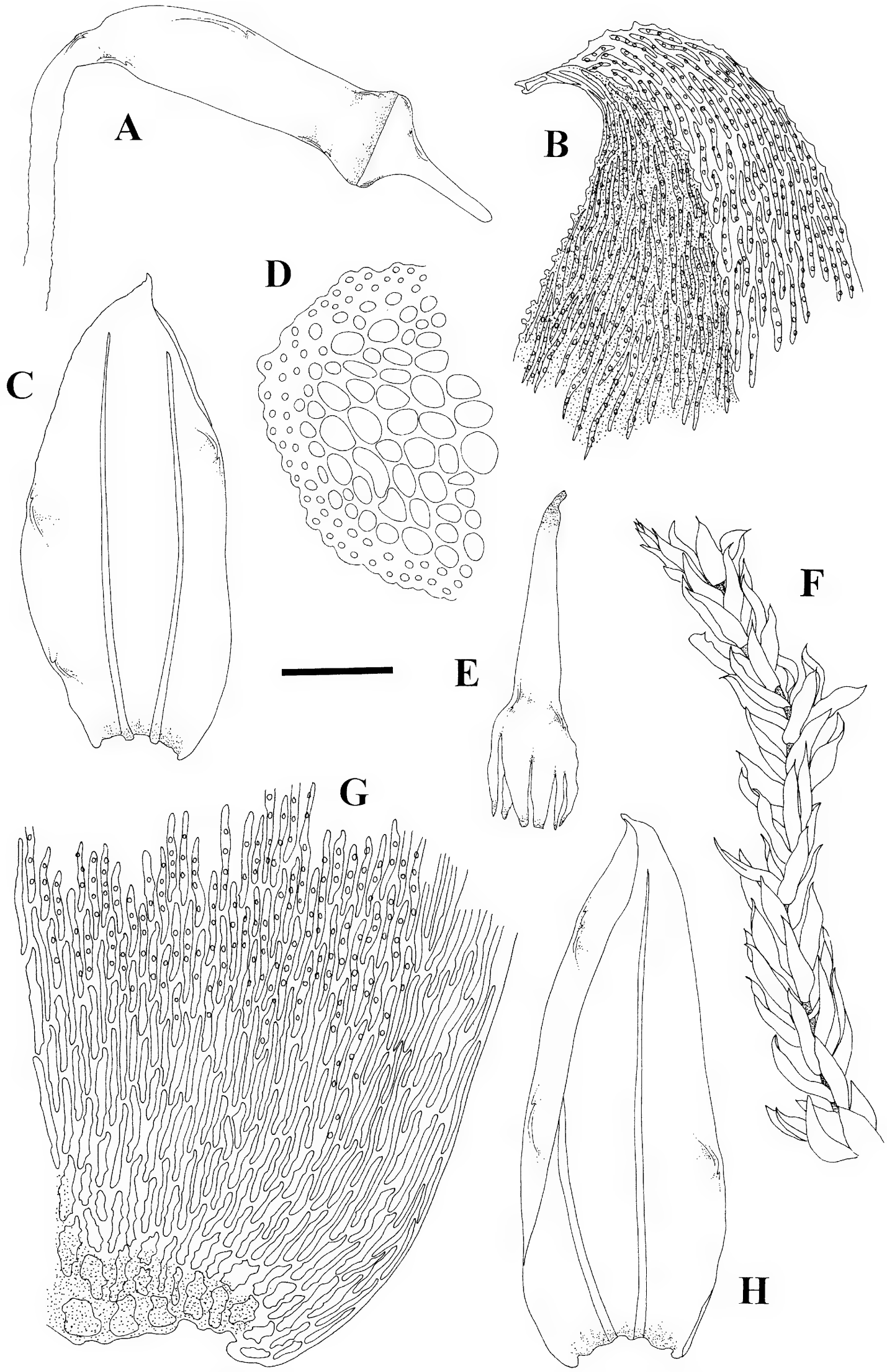


Figure 179. *Hypnella diversifolia*. A. Seta, capsule, and operculum. B. Leaf apex. C & H. Leaves. D. Stem in cross section. E. Calyptra. F. Habit. G. Basal and alar cells. Scale in mm: bar = 0.05 (B, G); bar = 0.06 (D); bar = 0.28 (C, H); bar = 0.6 (A, E); bar = 1.56 (F). A, E from *Crosby & Crosby 6043*; F from *Allen 5773*; all other figure parts from *Allen 12717*.

Hookeria pilotrichelloides Broth., Trans. Linn. Soc. London, Bot. 6: 92. 1901. *Hypnella pilotrichelloides* (Broth.) Broth., Nat. Pflanzenfam. I(3): 950. 1907. *Hookeria pilotrichoides* Broth. *in* Wijk, Margad. & Florsch., Regnum Veg. 26: 486. 1962, orthographic error. Protologue. [Guyana] Mount Roraima, Ledge, 7500–8000 ft., *McConnell & Quelch 337*.

Hypnella brotheri Herzog, Biblioth. Bot. 87: 138. 1916. Protologue. Bolivia. Auf feuchtem Waldboden beim Sillar, ca. 1800 m, [*Herzog*] *No. 2745*.

Neohypnella mucronifolia E. B. Bartram, Contr. U.S. Natl. Herb. 26: 104. 1928. *Pseudohypnella mucronifolia* E. B. Bartram *ex* W. H. Welch & H. A. Crum, Bryologist 62: 174. 1960, invalid name, error for *Neohypnella mucronifolia*. Protologue. On tree, La Palma, Province of San José, Costa Rica, altitude about 1600 meters, *Paul C. Standley*, February 3, 1924, *no. 33077*. Types. Costa Rica. La Palma, Province of San José; altitude about 1600 meters, February 3, 1924, *Paul C. Standley No. 33077* (FH, holotype; NY, S, US, isotypes).

Plants medium-sized to robust, 3–15 cm long, yellow green, golden reddish, in glossy, lax mats or pendent masses. Stems prostrate, sparsely to irregularly pinnately branched, red; stems in cross section with epidermis of 2–3 rows of small, thick-walled, red cells, cortical cells enlarged, firm-walled, yellowish to hyaline, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2 cells long, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids not commonly encountered, on branches or stems in contact with substrate, from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect to erect-spreading when dry, little changed when wet, oblong to oblong-lanceolate, 0.9–1.4 mm long, acute to rounded-acute, apices often recurved, concave, rounded to the insertions, not decurrent; margins entire at base, papillose-roughened to serrulate above, plane, erect or incurved; costae double, strong, diverging throughout, 2/3–3/4 the leaf length, at times ending in a projecting spine; cells pluripapillose with 2–6 simple or branched papillae, more or less seriately arranged over the lumina, linear-flexuose, 34–50 × 3 µm, thick-walled, usually porose, lower cells somewhat longer; basal cells across the insertions enlarged, rectangular, strongly porose, yellowish to reddish; alar cells undifferentiated. Asexual reproductive structures not seen. Dioicous. Perigonia and perichaetia sessile along stems and branches. Setae elongate, flexuose, 11–20 mm long, red to red brown, papillose-scabrous. Capsules erect to inclined, ovoid-cylindrical to cylindrical, 2.0 mm long, neck moderately developed; exothecial cells at mouth in 2–3 rows, reddish, quadrate to shortly oblate, yellowish, long-rectangular, thick-walled below, not collenchymatous; stomata rudimentary, on neck; opercula conic-rostrate, 1 mm long; annuli rudimentary, deciduous; peristome diplolepideous; exostome teeth erect to recurved when wet, incurved when dry, narrowly triangular, dorsal (outer) surface hyaline, cross-striate at base, papillose above, trabeculae well developed, zigzag median line faint, ventral (inner) surface yellowish, narrower than the dorsal surface, lightly papillose, trabeculae moderately developed; endostome as long as the exostome, hyaline to yellowish, lightly papillose throughout, basal membranes high, segments broad, weakly keeled, not or lightly perforate, cilia absent or vestigial. Spores rounded to oval, 10–16 µm, faintly papillose. Calyptrae mitrate, red and roughened above, yellowish and smooth below, irregularly lobed at base, 2.0–2.5 mm long.

Illustrations. Herzog (1916, Fig. 61); Bartram (1928a, Fig. 34); Welch (1971b, Figs. 231–234); Allen (1986, Figs. 30–37); Florschütz-de Waard (1986, Fig. 114); Churchill and Linares (1995, Fig. 40 a, b [left leaf], e; not b [right leaf], c, d); Buck (1998, Pl. 28 7–13). Figure 179.

Habitat. On tree trunks and branches, shrubs, and vines, often pendent, epiphyllous, on rotting logs, soil and humus on trail and road banks, rarely on moist rock cliffs, occasionally in hummingbird nests; [70–]650–2354 m.

Distribution in Central America. HONDURAS. Olancho: *Allen 12717* (MO). NICARAGUA. Granada: *Croat 39145* (MO); Jinotega: *Stevens 11387A* (HNMN, MO); Matagalpa: *Castro 2520B* (MO). COSTA RICA. Alajuela: *Lyons 654B* (MO); Cartago: *Crosby & Crosby 5762* (MO); Heredia: *Standley & Valerio 52167* (FH, US); Limón: *Standley 36570* (FH, US); Puntarenas: *Lyon 57* (CR, MO); San José: *Crosby 9739* (MO). PANAMA. Bocas del Toro: *Allen 5773* (MO); Chiriquí: *Allen 5484* (MO).

World range: Central America; Caribbean; Western and Northern South America.

Hypnella diversifolia is a fairly large, attractive species, with a glossy, golden red color, that often occurs pendent from branches and twigs. In Central America the species is typically found in high el-

evation cloud forests. It has dark stems with usually well-spaced leaves. Caribbean material of the species has large, foliose pseudoparaphyllia (Buck 1998), but Central American plants have only scale leaves on their branch buds. The leaves in Central American material are consistently oblong-lanceolate, with distinctly recurved apices; however, in South American material the leaves are shorter, not usually recurved at the apex, and oblong. The leaf cells in *H. diversifolia* are linear-flexuose throughout and are pluripapillose except at the extreme base. The papillae are more or less uniseriately arranged, and occasionally they are branched. The setae in *H. diversifolia* are long and scabrous, and the capsules erect to inclined.

The exostome teeth of *Hypnella diversifolia* are considerably different from the other members of *Hypnella* in being yellowish white in color and hygrocastique. Furthermore, the ventral (inner) surfaces of the exostome teeth are narrower than the dorsal (outer) surfaces. While all members of the genus have exostome teeth that are cross-striate on the lower dorsal surface, in *H. diversifolia* the striae reach the median line. In the other members of the genus the cross-striae fail to reach the median line, and thus a median furrow is present. This type of exostome tooth modification in *H. diversifolia* may be the result of its adaptation to an epiphytic habitat. Nevertheless, despite its color and hydrocastique motion, the *H. diversifolia* peristome is hookeriaceous in form and not daltoniaceous as suggested by Florschütz-de Waard (1986).

Hypnella diversifolia differs from most other members of the genus in its usually epiphytic habit and (except for *H. guayanensis*) golden red color. *Hypnella pilifer*, *H. leptorrhyncha*, and *H. ambrosia* also differ from *H. diversifolia* in having long-acuminate to piliferous leaves. Although similar in color, *H. guayanensis* differs from *H. diversifolia* in its smaller leaves (0.7–1.0 mm long) that are mostly ecostate and have cells that can be entirely or partly smooth. *Hypnella punctata* most distinctly differs from *H. diversifolia* in its long, acute leaf apices. Although *H. pallescens* comes out in the key next to *H. diversifolia*, the two species are quite different. In *H. pallescens* the plants are usually glaucous green; the smaller leaves (0.5–1.0 mm long) are obtuse; and leaf cells have mostly multi-branched papillae. Sporophytically, the presence in *H. pallescens* of reddish, furrowed exostome teeth and tuberculate to scabrous capsule necks separates it from *H. diversifolia*.

3. *Hypnella guayanensis* B. H. Allen & W. R. Buck *in* W. R. Buck, Mem. New York Bot. Gard. 64: 190. 1990. Protologue. Guyana. Upper Potaro River Region: Mt. Wokomung base camp and vic., 05°05′N, 59°50′W, 1070 m, moist tropical forest, epiphytic, 8 Jul. 1989, *Boom & Samuels 9131*. Type. Guyana. Upper Potaro River region, Mt. Wokomung Base Camp and vicinity, 05°05′N, 59°50′W. Moist tropical forest. 1070 m elev. Epiphytic, 8 Jul. 1989, *Boom & Samuels 9131* (MO, isotype).

Plants small to medium-sized, 3–5 cm long, golden reddish, yellow green, or pale green, in glossy, dense mats. Stems prostrate, densely, irregularly, or subpinnately branched, dark red; stems in cross section with epidermis of 2–3 rows of small, thick-walled, red cells, cortical cells enlarged, firm-walled, yellowish to hyaline, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2 cells long, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Stem leaves erect, widely spaced, ovate, broadly acute, 0.7–1.0 mm long, concave, rounded to the insertions, not decurrent; margins entire or with a few small, widely spaced serrations, erect to broadly incurved; costa none or occasionally double and short, less than 1/3 the leaf length; cells from leaves on single plants variably ornamented (entirely smooth, entirely pluripapillose, or a mix of smooth and pluripapillose), papillae simple or branched, more or less biseriately arranged over the lumina, upper cells linear-flexuose, 60–100 × 4–7 µm, usually thick- or firm-walled, often porose, occasionally thin-walled; basal cells across the insertions enlarged, rectangular, strongly porose, yellowish to reddish; alar cells undifferentiated. Branch leaves erect-spreading to weakly homomallous, dense, oblong-lanceolate, bluntly acute, 0.6–0.9 mm long. Asexual reproductive structures not seen. Autoicous. Perigonia and perichaetia sessile along stems and branches. Setae elongate, flexuose, 15–25 mm long, red to red brown, smooth below, papillose above. Capsules red, erect to inclined, ovoid-cylindrical, 1–2 mm long, neck well developed, strongly tuberculate; exothecial cells at mouth reddish, quadrate to shortly oblate in 2–3 rows, red, rectangular, strongly collenchymatous below; stomata rudimentary, on neck; opercula conic-rostrate, 1 mm long; annuli

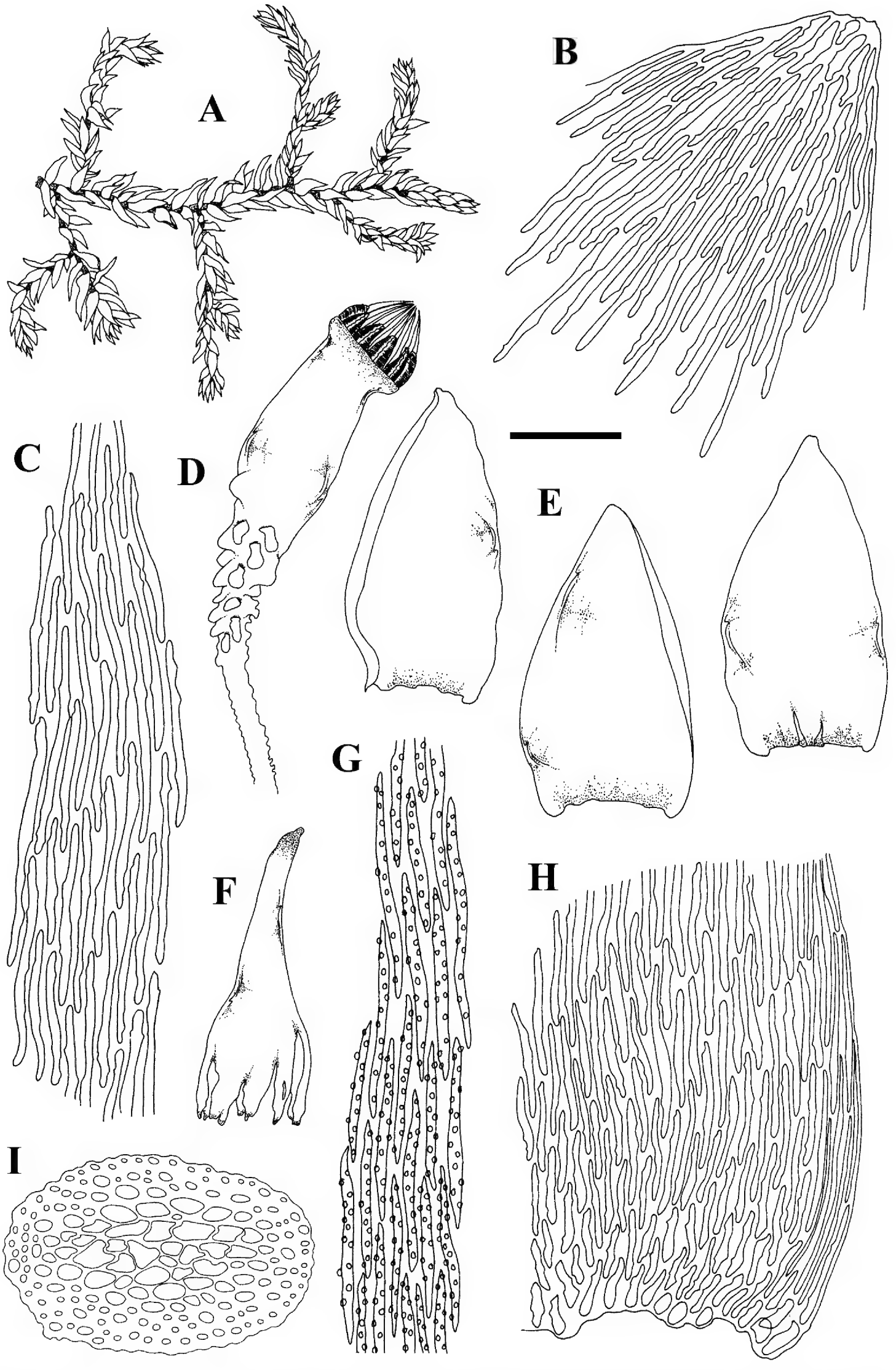


Figure 180. *Hypnella guayanensis*. A. Habit. B. Leaf apex. C. Smooth median leaf cells. D. Seta and capsule. E. Leaves. F. Calyptra. G. Papillose median leaf cells. H. Basal and alar cells. I. Stem in cross section. Scale in mm: bar = 0.05 (B, C, G, H); bar = 0.08 (I); bar = 0.2 (E); bar = 0.6 (D, F); bar = 1.96 (A). All figure parts from *Allen 23442*.

rudimentary; peristome diplolepideous; exostome teeth erect to incurved when wet, outcurved when dry, narrowly triangular, dorsal (outer) surface dark red, densely cross-striate below, papillose above, with wide, yellow, median furrows, zigzag median line faint, ventral (inner) surface yellowish, lightly papillose, trabeculae moderately developed; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, weakly keeled, not or lightly perforate, cilia absent or vestigial. Spores rounded to oval, 10–15 µm, faintly papillose. Calyptrae mitrate, red and roughened above, yellowish and smooth below, deeply lobed at base, 2.0 mm long.

Illustrations. Buck (1990, Figs. 6–13). Figure 180.

Habitat. On tree trunks, logs, fallen branches, vines, roots, humus in forest, and sandstone boulders; 810–1160 m.

Not known from Central America.

World range: Northern South America.

Hypnella guayanensis is presently known only from the Guayana Highlands area of Venezuela, Guyana, and Suriname. This remarkable species differs from all other members of the genus in having leaves that are almost always ecostate. Occasionally a few leaves can be found with very short, double costae. An even more noteworthy feature of the species, however, is the incredible variability of its leaf cell ornamentation. On a single stem some leaves can have entirely smooth cells, while others have entirely pluripapillose cells. Although single branches usually have leaves that are either smooth or pluripapillose, sometimes a branch can have some leaves with pluripapillose cells and others with smooth cells. The leaves with smooth cells are typically golden reddish and have very thick-walled, porose cells, while those with pluripapillose cells are often pale green and have thin-walled, weakly porose cells. Papillose leaf cells have the papillae biseriately arranged over the lumina.

Hypnella diversifolia is similar to *H. guayanensis* in color, and both species often grow epiphytically. It differs from *H. guayanensis* in having long, double costae and leaf cells that are consistently pluripapillose with the papillae uniseriately arranged over the lumina. *Hypnella pallescens* is similar to the pluripapillose form of *H. guayanensis* in size, color, leaf shape, and in having tubercular to scabrous capsule necks. The costae in *H. pallescens* are short for the genus (1/3–1/2 the leaf length), but they are always present. It further differs from *H. guayanensis* in having consistently pluripapillose leaf cells with the papillae often stellately branched.

4. *Hypnella leptorrhyncha* (Hook. & Grev.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 366. 1877. *Hookeria leptorrhyncha* Hook. & Grev., Edinburgh J. Sci. 2: 228. 1825 [*leptorhyncha*]. Protologue. Island of St. Vincent's, *Rev. Guilding*. Types. St. Vincent, Dr. Greville, 1832 (BM, isotype).

Hookeria filiformis Hook. & Grev., Edinburgh J. Sci. 2: 228. 1825. *Hypnella filiformis* (Hook. & Grev.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 366. 1877. Protologue. Island of Guadeloupe, comm. Professor Sprengel. Type. Guadeloupe, *H*[*ooker*]. *1932* (BM, holotype).

Hookeria cupressiformis Müll. Hal., Syn. Musc. Frond. 2: 215. 1851. Protologue. Insula Trinidad Antillarum, ubi monte Tocuche copiose legit *Crüger*, 1847. mens. Decbr., Jan. et Mart. Types. Insula Trinidad Antill. *Crüger* lg., Hb. Müll. Hal. (BM, isotype); Monte Tocuche, *Cruger leg.* (BM, isotype); Trinidad. Tocuche. *Crüger*, 1847 (MO, isotype).

Hookeria pseudo-pilifera Hampe, Linnaea 25: 362. 1852. *Hypnella pseudo-pilifera* (Hampe) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 366. 1877. Protologue. [Puerto Rico] In arboribus putridis, [*Schwanecke*] *36*. Type. In sylva mont. Portoricenses, leg. *Schwanecke* (BM, holotype).

Hookeria erythrochaete Schimp. *ex* Besch., Ann. Sci. Nat., Bot., sér. 6, 3: 240. 1876. *Hypnella erythrochaete* (Schimp. *ex* Besch.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 366. 1877. Protologue. Guadeloupe (*L'Herminier*, in herb. Schimp.).

Hookeria philonotula Müll. Hal., Linnaea 42: 496. 1879. *Hypnella philonotula* (Müll. Hal.) Kindb., Enum. Bryin. Exot. 99. 1891. Protologue. Venezuela. [*Fendler*] *130*.

Plants small and slender, 1–3 cm long, reddish, green, or pale green, in dull mats. Stems prostrate, irregularly branched, dark red; stems in cross section with a single row of enlarged hyalodermis cells, epidermis of 2–3 rows of small, thick-walled, red cells, cortical cells enlarged, firm-walled, yellowish to hyaline, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs

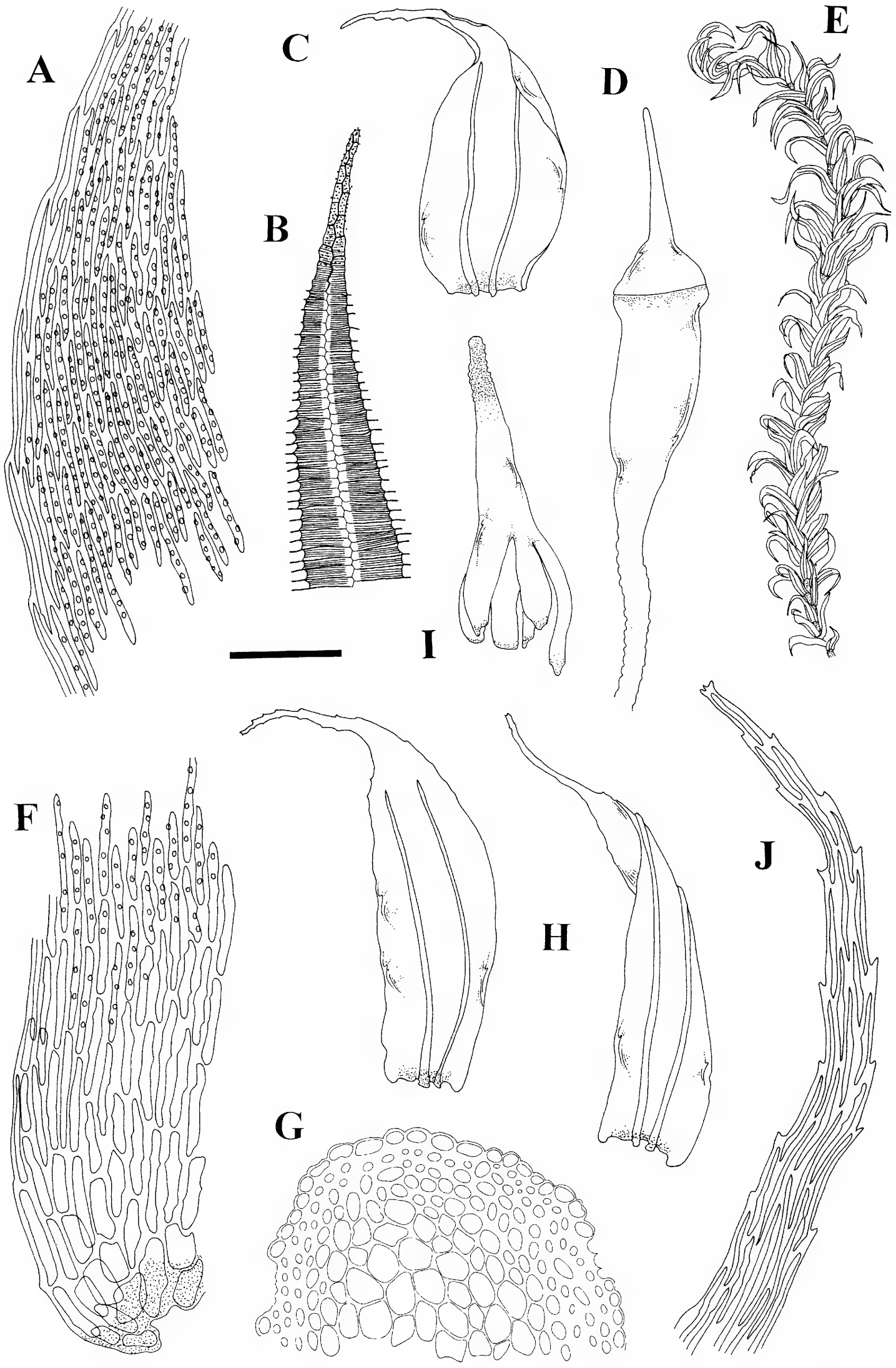


Figure 181. *Hypnella leptorrhyncha*. A. Median leaf cells and margin. B. Exostome, dorsal (outer) surface. C & H. Leaves. D. Seta, capsule, and operculum. E. Habit. F. Basal and alar cells. G. Stem in cross section. I. Calyptra. J. Leaf apex. Scale in mm: bar = 0.05 (A, F, J); bar = 0.08 (G); bar = 0.09 (B); bar = 0.28 (C, H); bar = 0.5 (D, I); bar = 1.56 (E). B, D, I from *Steere 4308*; all other figure parts from *Crosby 3442*.

2 cells long, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect-spreading to falcate-secund when dry, oblong-lanceolate, ovate-lanceolate to lanceolate, 0.7–1.5 mm long, concave, gradually or abruptly long-acuminate, rounded to the insertions, not decurrent; margins serrate to serrulate above, serrulate to entire below, plane to erect, weakly bordered by 1–2 rows of smooth cells; costae double, strong, 3/4 the leaf length; cells pluripapillose with 2–8 more or less seriately arranged papillae over the lumina, smooth in 1–2 marginal rows, oblong to linear-flexuose, 30–60 × 3–4 µm, firm-walled; basal cells near the insertions smooth, often porose, cells across the insertions enlarged, rectangular, porose, yellowish to reddish; alar cells undifferentiated. Asexual reproductive structures not seen. Dioicous. Perigonia and perichaetia sessile along stems and branches. Setae elongate, flexuose, 10–15 mm long, red to red brown, smooth below, papillose above. Capsules red, more or less erect, inclined to pendent, ovoid-cylindrical, 1–2 mm long, neck well developed; exothecial cells at mouth reddish, quadrate to shortly oblate in 2–3 rows, yellowish red, rectangular to oblong, collenchymatous below; stomata rudimentary, on neck; opercula conic-rostrate, 1 mm long; annuli rudimentary; peristome diplolepideous; exostome teeth erect to incurved when wet, outcurved when dry, narrowly triangular, dorsal (outer) surface dark red, densely cross-striate below, papillose above, with wide, yellow, median furrows, zigzag median line faint, ventral (inner) surface yellowish, lightly papillose, trabeculae moderately developed; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, keeled, not or lightly perforate, cilia absent or vestigial. Spores rounded to oval, 12–15 µm, faintly papillose. Calyptrae mitrate, reddish and roughened above, yellowish and smooth below, lobed at base, 1.0–1.5 mm long.

Illustrations. Hooker and Greville (1825, Pl. 5); Welch (1969, Figs. 157–163, as *Hypnella filiformis*); Welch (1971b, Figs. 164–172); Allen (1986, Figs. 7–14); Duarte Bello (1997, Pl. 286, as *Hypnella filiformis*); Buck (1998, Pl. 28 14–20). Figure 181.

Habitat. On tree trunks, fallen branches, and rotting logs; 792–1074 m.

Not known from Central America.

World range: Caribbean; Northern South America.

Hypnella leptorrhyncha is presently known from the Caribbean, Trinidad, and Venezuela. It is a slender species, with leaves that are extremely variable in shape, apex form, and costal length. Although the extreme expressions in this variation have been segregated into several taxa, there are only two major forms of the species, and these are nomenclaturally centered on *H. leptorrhyncha* and *H. filiformis*. The *H. leptorrhyncha* form has narrow leaves that are gradually and slenderly acuminate, while the *H. filiformis* expression has broader leaves that are more or less abruptly contracted to a filiform, flexuose acumen. There are, however, numerous collections that are intermediate in form between the two, and sometimes single collections can have both types of leaves. *Hypnella leptorrhyncha* often has falcate to secund leaves with long, narrow, flexuose leaf cells and strong double costae that are smooth on the dorsal surface, taper at the ends, and rarely project at the tips. Its leaf margins are weakly bordered by 1–2 rows of smooth cells, and they are serrate to serrulate by projecting cell end-walls.

Hypnella ambrosia and *H. pilifera* can be confused with *H. leptorrhyncha* because they all have long-acuminate to piliferous leaves. In *H. ambrosia*, however, the marginal leaf cells are short, broad, and more or less rectangular in shape. In addition, the costae are serrate on the upper dorsal surface and strongly project as a multicellular spine at the tips. *Hypnella pilifer* differs from most forms of *H. leptorrhyncha* in having leaves that are abruptly rounded above into subpiliferous to piliferous apices. As noted above, however, there are some forms of *H. leptorrhyncha* that have leaves abruptly contracted to a filiform, flexuose acumen. The leaves of *H. pilifer* differ from all forms of *H. leptorrhyncha* in having cells with high, prominent papillae, papillose marginal cells, and margins serrulate due to lateral, projecting papillae.

5. *Hypnella pallescens* (Hook.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 365. 1877. *Hookeria pallescens* Hook., Musci Exot. 1: 38. 1818. Protologue. [Venezuela] Ad ripam fluminis Orinoco prope Esmeraldam, locis opacis, *Humboldt et Bonpland*. Types. S.

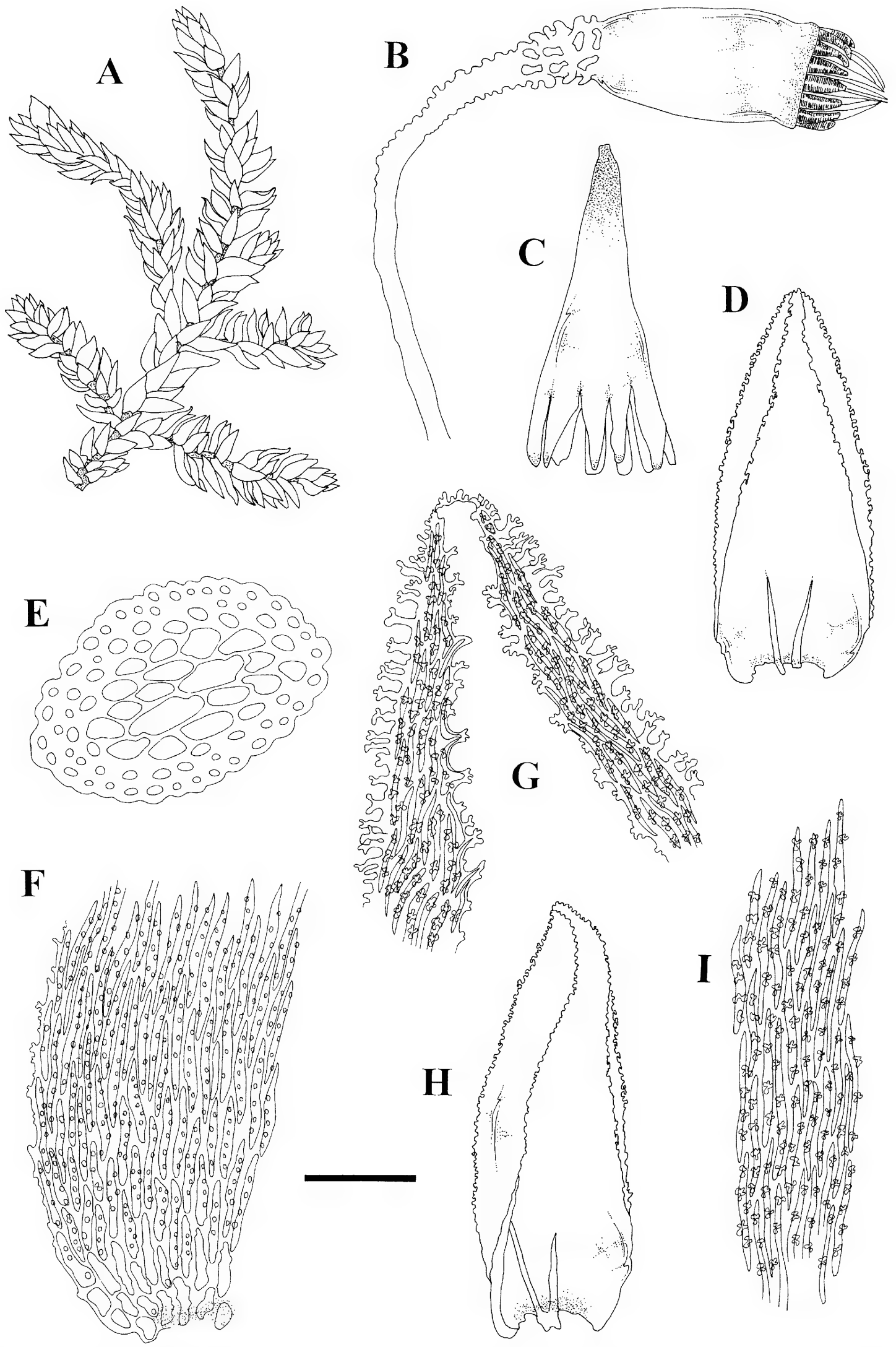
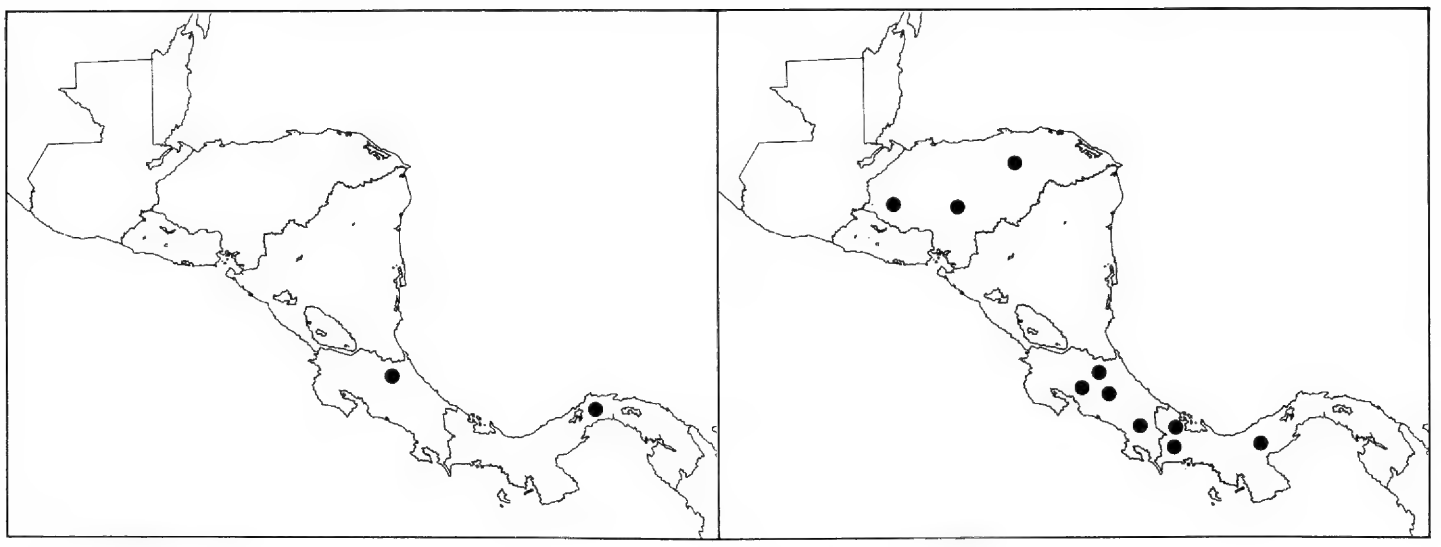


Figure 182. *Hypnella pallescens*. A. Habit. B. Seta and capsule. C. Operculum. D & H. Leaves. E. Stem in cross section. F. Basal and alar cells. G. Leaf apex. I. Median leaf cells. Scale in mm: bar = 0.06 (E–G, I); bar = 0.2 (D, H); bar = 0.5 (B, C); bar = 1.56 (A). All figure parts from *Allen 23737*.



Hypnella pallescens *Hypnella pilifera*

Am. *Humboldt 33. H*[*ooker*] *1509*, Hook. Musc. Exot. t. 38, original sp^{m} (BM, holotype; E, NY, isotypes).

Hookeria cymbifolia Hampe, Linnaea 25: 362. 1852. *Hypnella cymbifolia* (Hampe) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 365. 1877. Protologue. [Puerto Rico] Ad arbor truncos putridos, [*Schwanecke*] *35*. Type. Ad arb. sylva-mont., Portoricenses, *Schwanecke* [Herb. Hampe] (BM, holotype).
Hookeria spruceana Hampe *in* M. Fleisch., Hedwigia 63: 215. 1922, invalid name, lacks a description.
Pseudohypnella guianensis P. W. Richards, Bull. Misc. Inform. Kew 8: 336. 1934. Protologue. Guyana. Moraballi Creek, on log in Wallaba forest, *Richards 407*.

Plants small to medium-sized, 3–5 cm long, usually pale green and glaucous, but becoming golden reddish to yellow green in direct sunlight, in dense or loose mats. Stems prostrate, densely and irregularly or subpinnately branched, green when young, becoming dark red with age; stems in cross section with epidermis of 2–3 rows of small, thick-walled, red cells, cortical cells enlarged, firm-walled, yellowish to hyaline, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2 cells long, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, sparsely and irregularly branched. Stem leaves erect, widely spaced, ovate to oblong-lanceolate, broadly rounded, obtuse, at times lightly cucullate, 0.7–1.0 mm long; margins erect to incurved. Branch leaves erect-spreading to weakly homomallous, dense, oblong-lanceolate, 0.6–0.9 mm long, concave, bluntly acute, rounded to the insertions, not decurrent; margins entire or with a few small, widely spaced serrations, erect to broadly incurved; costae double, short, 1/4–1/2 the leaf length; cells pluripapillose except at very base of leaf, papillae large, simple or more often stellately branched, more or less biseriately arranged over the lumina, linear-flexuose, 50–80 × 4–7 μm, firm-walled, not porose; basal cells across the insertions enlarged, rectangular, porose, yellowish to reddish; alar cells undifferentiated. Asexual reproductive structures not seen. Autoicous. Perigonia and perichaetia sessile along stems and branches. Setae elongate, flexuose, 10–20 mm long, red to red brown, smooth below, papillose to scabrous above. Capsules red, erect to inclined or pendent, ovoid-cylindrical, 1–2 mm long, neck well developed, strongly tuberculate; exothecial cells at mouth reddish, quadrate to shortly oblate in 2–3 rows, red, rectangular, strongly collenchymatous below; stomata rudimentary, on neck; opercula conic-rostrate, 0.7–1.0 mm long; annuli complex, adhering to operculum after dehiscence; peristome diplolepideous; exostome teeth erect to incurved when wet, recurved when dry, narrowly triangular, dorsal (outer) surface dark red, densely cross-striate below, papillose above, with wide, yellow, median furrows, zigzag median line faint, ventral (inner) surface yellowish, lightly papillose, trabeculae moderately developed; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, weakly keeled, not or lightly perforate, cilia absent or vestigial. Spores rounded to oval, 8–14 μm, faintly papillose. Calyptrae mitrate, red and roughened above, yellowish and smooth below, deeply lobed at base, 1.5–2.0 mm long.

Illustrations. Hooker (1818, Pl. 38); Richards (1934, Fig. 6); Welch (1969, Figs. 148–156, as *Hypnella cymbifolia*); Allen (1986, Figs. 22–29); Churchill and Linares (1995, Fig. 40 b (right leaf), c, d, as *Hypnella diversifolia*); Duarte Bello (1997, Pl. 285, as *Hypnella cymbifolia*); Buck (1998, Pl. 28 1–6); Buck (2003, Fig. 90). Figure 182.

Habitat. On tree trunks, roots, rotting logs, and damp roadside banks; 700–1350 m.

Distribution in Central America. COSTA RICA. Heredia: *Nee 14362* (CR, MO). PANAMA. Panamá: *Allen 9031* (MO).

World range: Caribbean; Central America; Western and Northern South America, Brazil.

Hypnella pallescens is a medium-sized species with dark red stems and typically a glaucous, pale green color. It has ovate to oblong-lanceolate leaves with erect to incurved margins and rounded apices that are often subcucullate to weakly cucullate. Distinctive features of the species include the large, generally stellately branched papillae in one or two rows on the linear-flexuose leaf cells, and weak double costae that extend only 1/4–1/2 the leaf length. It is an autoicous species and collections commonly have sporophytes. The long setae are strongly papillose to scabrose above. The oblong-cylindric capsules are usually inclined to pendent and tuberculate on well-developed necks, and they have strongly collenchymatous exothecial cells. As with most species in the genus, the xerocastique peristomes have strongly furrowed, densely cross-striate exostome teeth, and the endostome has broad, keeled segments, high basal membranes, and no cilia.

Hypnella diversifolia and *H. guayanensis* are the only other *Hypnella* species that can be confused with *H. pallescens*, because they have similarly shaped, subapiculate to obtuse leaves. Plants of *H. diversifolia* differ from those of *H. pallescens* in their consistently reddish yellow color, epiphytic habitat, and subacute, apiculate leaves. In addition, the leaves have long, double costae and shorter, mostly non-branched papillae. *Hypnella diversifolia* is also a dioicous species with non-tuberculate capsules and yellowish white, non-furrowed exostome teeth. *Hypnella guayanensis* and *H. pallescens* are similar in size, color, leaf shape, and in having tuberculate to scabrous capsule necks. However, *H. guayanensis* has mostly ecostate leaves. Furthermore, on some leaves in *H. guayanensis* the leaf cells are entirely smooth, while in others they are entirely or partly pluripapillose. Often entire branches have one or the other type of cell ornamentation, but occasionally single branches have some leaves with smooth cells and others with entirely or partly pluripapillose cells.

6. *Hypnella pilifera* (Hook. & Wilson) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 366. 1877. *Hookeria pilifera* Hook. & Wilson, London J. Bot. 3: 160. 1844. Protologue. [Brazil] 89. *H. pilifera nov. sp.* On the face of moist rock, Organ Mountains. March 1837. [*Gardner*] *n. 15*, (2). Types. On the face of a moist rock, Organ M^{ts}, March 1837, *Gardner 15* (BM, holotype; BM [5], E, FH, MICH, NY, isotypes).

Hookeria papillata Taylor, London J. Bot. 7: 283. 1848, illegitimate homonym, not *Hookeria papillata* Mont., 1845. *Hookeria taylorii* Müll. Hal., Syn. Musc. Frond. 2: 222. 1851, new name for *Hookeria papillata* Taylor. *Hypnella taylorii* (Müll. Hal.) M. Fleisch., Hedwigia 63: 215. 1922. *Hookeriopsis taylorii* (Müll. Hal.) Wijk & Margad., Taxon 9: 190. 1960. Protologue. [Ecuador] On Pichincha. *Prof. W. Jameson*. 8th Aug., 1847.

Hookeria araucariae Müll. Hal., Hedwigia 39: 282. 1900. *Hypnella araucariae* (Müll. Hal.) Broth. *ex* Paris, Coll. Nom. Broth. 16. 1909. Protologue. Brasilia, Sa. Catharina, Serra Geral, ad marginem in solo humido, Septbr. 1890, c. fr. maturis: *E. Ule, Col. No. 1031*; in eadem Serra in terra araucarieti, Januario 1890, c. fr. juvenilibus: *E. Ule, Coll. No. 884*. Types (see Crosby *et al.* 1985). Brasilia, Sao Catharina, Serra Geral, in eadem serra in terra araucarieti, Januario 1890, c. fr. juvenilibus: *E. Ule, Coll. No. 884* (H, lectotype; PC, isolectotype).

Hookeria caudifrons Müll. Hal., Hedwigia 39: 281. 1900. *Hypnella caudifrons* (Müll. Hal.) Broth. *ex* Paris, Coll. Nom. Broth. 16. 1909. Protologue. Brazil. Brasilia, Minas Geraës, Serra Itabira de Campo, ad rivulum in lapidibus, Febr. 1892: *E. Ule, Coll. No. 1469 et 1471*. Types (see Crosby *et al.* 1985). *E. Ule 1471* (H, lectotype); *E. Ule 1469* (H, syntype).

Hookeria pseudo-pilifera Müll. Hal., Hedwigia 39: 282. 1900, illegitimate homonym, not *Hookeria pseudopilifera* Hampe, 1853. *Hookeria apiahiensis* Paris, Index Bryol. (ed. 2) 2: 236. 1904, new name for *Hookeria pseudo-pilifera* Müll. Hal. Protologue. Brasilia, São Paulo, prope Apiahi, Junio 1879, *Juan J. Puiggari*. Type. *Juan J. Puiggari 633* (H, JE, L, PC, S, isotypes).

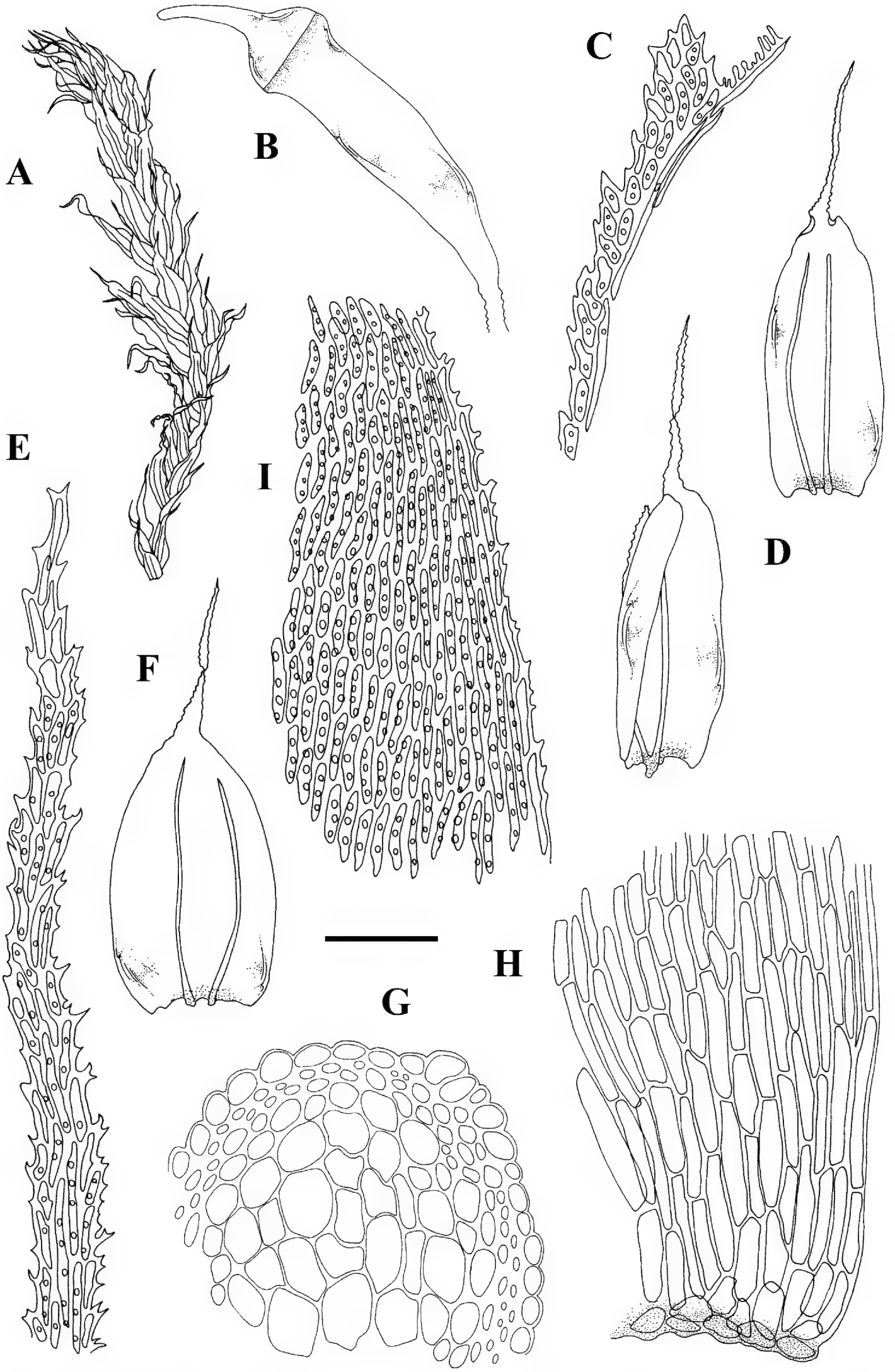


Figure 183. *Hypnella pilifera*. A. Habit. B. Seta, capsule, and operculum. C. Costal crest. D & F. Leaves. E. Leaf apex. G. Stem in cross section. H. Basal and alar cells. I. Upper leaf cells and margin. Scale in mm: bar = 0.05 (C, E, I); bar = 0.06 (H); bar = 0.08 (G); bar = 0.5 (D, F); bar = 0.9 (B); bar = 1.56 (A). B from *Valerio 199*; all other figure parts from *Allen 12013*.

Plants medium-sized, 1–5 cm long, green, pale green, or yellowish green, in dull mats. Stems prostrate, irregularly branched, dark red; stems in cross section with a single row of enlarged hyalodermis cells, epidermis of 2–3 rows of small, thick-walled, red cells, cortical cells enlarged, firm-walled, yellowish to hyaline, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2 cells long, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect and more or less crispate when dry, erect-spreading when wet, elliptic to oblong-lanceolate or linear-lanceolate, 1.5–2.0 mm long, concave, rounded at the apex and abruptly subulate, rounded to the insertions, not decurrent; margins serrulate below by projecting end walls, serrate to dentate above by serrulate projecting end walls and lateral projecting papillae, plane or erect; costae double, strong, 3/4 the leaf length, usually projecting at tips by 1–3-celled dorsal crests or spines; upper and median cells pluripapillose with 2–6 more or less seriately arranged, often high and curved papillae, oblong to linear-flexuose, 20–40 × 3–4 μm, firm-walled; basal cells enlarged, smooth, long-rectangular to elongate-hexagonal, cells across the insertions enlarged, rectangular, smooth or weakly porose, reddish, basal marginal cells narrow and elongate forming a more or less distinct border; alar cells undifferentiated. Asexual reproductive structures not seen. Autoicous. Perigonia and perichaetia sessile along stems and branches. Setae elongate, flexuose, 15–35 mm long, red to red brown, smooth below, weakly papillose above. Capsules red, inclined to pendent, ovoid-cylindrical to cylindrical, 2–3 mm long, neck well developed; exothecial cells at mouth quadrate to shortly oblate in 2–3 rows, reddish, yellowish red, rectangular to oblong, collenchymatous below; stomata rudimentary, on neck; opercula conic-rostrate, 0.7–1.0 mm long; annuli rudimentary; peristome diplolepideous; exostome teeth erect to incurved when wet, recurved when dry, narrowly triangular, dorsal (outer) surface dark red, densely cross-striate below, papillose above, with wide, yellow, median furrows, zigzag median line faint, ventral (inner) surface yellowish, lightly papillose, trabeculae moderately developed; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, keeled, not or lightly perforate, cilia absent or vestigial. Spores rounded to oval, 8–14 μm, faintly papillose. Calyptrae mitrate, reddish and roughened above, yellowish and smooth below, lobed at base, 3 mm long.

Illustrations. Welch (1972b, Figs. 13–25); Allen (1986, Figs. 15–21); Sharp *et al.* (1994, Fig. 621); Churchill and Linares (1995, Fig. 40 f–k); Gradstein *et al.* (2001, Fig. 167 J–O); Vaz and Costa (2006a, Figs. 98–104). Figure 183.

Habitat. On tree trunks and twigs, humus or moist soil, and rotting logs, branches, and trunks; 800–2850 m.

Distribution in Central America. HONDURAS. Francisco Morazán: *Morton 7215* (US); Lempira: *Allen 12013* (MO); Olancho: *Allen 12682* (MO). COSTA RICA. Cartago: *Gómez 18850* (MO); Heredia: *Standley & Valerio 49713* (FH, US); Puntarenas/Limón: *Davidse et al. 26097* (MO); San José: *Crosby 9672* (MO). PANAMA. Bocas del Toro: *Gómez et al. 22355* (MO); Chiriquí: *Croat 74883* (MO); Coclé: *Folsom et al. 5719* (MO, PMA, NY).

World range: Mexico; Central America; Western and Northern South America, Brazil.

Hypnella pilifera is a medium-sized species that differs from all other *Hypnella* species in having erect, more or less crispate leaves. This gives the plants an overall aspect very much like *Thamniopsis undata*. Plants of *H. pilifera* are usually green to pale green, and they have dark red stems with well-spaced leaves. The leaves are mostly elliptic to oblong-lanceolate below and abruptly rounded above to long, sharply serrate to denticulate subulae. The stem and branch apices in *H. pilifera* are swollen, and this, as well as the presence of long leaf subulae, gives the apices a distinct appearance not otherwise seen in *Hypnella*, but very similar to the leaf apices of *Stenodictyon wrightii.* Although the lower leaf margins of *H. pilifera* are entire to serrulate by projecting cell end walls, the upper margins are sharply serrulate to denticulate by both projecting end walls and long papillae. The upper leaf cells have numerous, high, often curved papillae, but the basal cells are smooth and enlarged in much the same way as *Thamniopsis* species. The costae are long and typically end in a dorsal spine or short dorsal crests. The setae are long and weakly papillose above. The oblong-cylindric capsules are usually inclined to pendent, smooth or papillose, on well-developed necks, and they have strongly collen-

chymatous exothecial cells. The xerocastique peristome has strongly furrowed, densely cross-striate exostome teeth, and the endostome has broad, keeled segments, a high basal membrane, and no cilia.

Hypnella ambrosia and *H. leptorrhyncha* are the only *Hypnella* species that can be confused with *H. pilifera*, because they have similarly shaped, long-acuminate to piliferous leaves. Plants of *H. ambrosia* resemble those of *H. pilifera* in having strong costae that usually project by two or more cells at the tip. *Hypnella ambrosia* differs, however, in having gradually and evenly long-acuminate leaves with short, broadly rectangular upper marginal cells that are serrulate only by projecting end walls. Most collections of *H. leptorrhyncha* differ from those of *H. pilifera* in having gradually long-acuminate leaves; however, *H. leptorrhyncha* sometimes has abruptly acuminate leaves. All plants of *H. leptorrhyncha*, though, have short, more or less obscure papillae, leaf margins that are serrulate by projecting end walls but otherwise smooth, and lower cells that are enlarged only at the very base of the leaf. The sporophytes of *H. leptorrhyncha* differ from those of *H. pilifera* in having shorter setae (10–15 mm vs. 15–35 mm).

7. *Hypnella punctata* Broth., Nat. Pflanzenfam. I(3): 949. 1907, new name for *Hookeria punctata* Hampe, Vidensk. Meddel. Dansk. Naturhist. Foren. Kjøbenhavn ser. 4, 1: 138. 1879, illegitimate homonym, not *Hookeria punctata* Hook. f. & Wilson, 1844. Protologue. [Brazil] Prope Rio de Janeiro c. *Dicrano* commixtam, *Glaziou s.n.* Type. Brasilia austral. Inter muscos (*Dicrano*) in [illegible] Rio de Janerio, [Herb. Hampe] (BM, holotype).

Plants trailing, green or greenish yellow. Stems irregularly branched, red, 2 cm long; stems in cross section with hyalodermis of enlarged, thin-walled cells, subepidermal cells small, thick-walled, cortical cells enlarged, firm-walled, yellowish to hyaline, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs not seen; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect-spreading to somewhat falcate when dry, oblong-lanceolate to lanceolate, 0.6–1.5 mm long, concave, acute to shortly acuminate, rounded to the insertions, not decurrent; margins serrate to serrulate above, serrulate to entire below, plane or erect, weakly bordered by 1–2 rows of smooth cells; costae double, strong, 3/4 the leaf length, often ending in forward-projecting spines; cells pluripapillose with 3–8, stout, often forked papillae, more or less seriately arranged over the lumina, mostly smooth, in 1–2 marginal rows, oblong to linear-flexuose, 30–40 × 3–4 μm, firm-walled; basal cells near the insertions smooth, often porose, cells across the insertions enlarged, rectangular, porose, yellowish to reddish; alar cells undifferentiated. Sporophytes unknown.

Illustrations. Allen (1986, Figs. 1–6). Figure 184.
Habitat. On ground, mixed with Dicranaceae.
Not known from Central America.
World range: Brazil.

Hypnella punctata is known only from the type locality in southeastern Brazil. It has acute, sometimes shortly acuminate leaves that cause it to key out near *H. diversifolia*, *H. guayanensis*, and *H. pallescens*. However, all those species have obtuse to round-apiculate leaves, and they do not appear closely related to *H. punctata.* On the other hand, *H. leptorrhyncha* appears very similar to *H. punctata* in having narrow, mostly lanceolate leaves that are obscurely bordered by long, narrow, more or less smooth cells. In addition, the leaves of both species have a similar areolation and serrate apices. The two species differ only in leaf apex shape and geography. In *H. punctata*, the apices are acute or occasionally shortly acuminate, and it is known only from southern Brazil. *Hypnella leptorrhyncha* has long, narrowly acuminate apices, and it is known from the Caribbean and Venezuela.

10. *Lepidopilidium* (Müll. Hal.) Broth., Nat. Pflanzenfam. I(3): 942. 1907. *Hookeria* Sm. sect. *Lepidopilidium* Müll. Hal., Hedwigia 39: 272. 1900.

Plants medium-sized, green, yellowish green, or golden reddish, in lax or dense mats. Stems prostrate, irregularly branched, complanate-foliate; stems in cross section with a hyalodermis, subepidermal

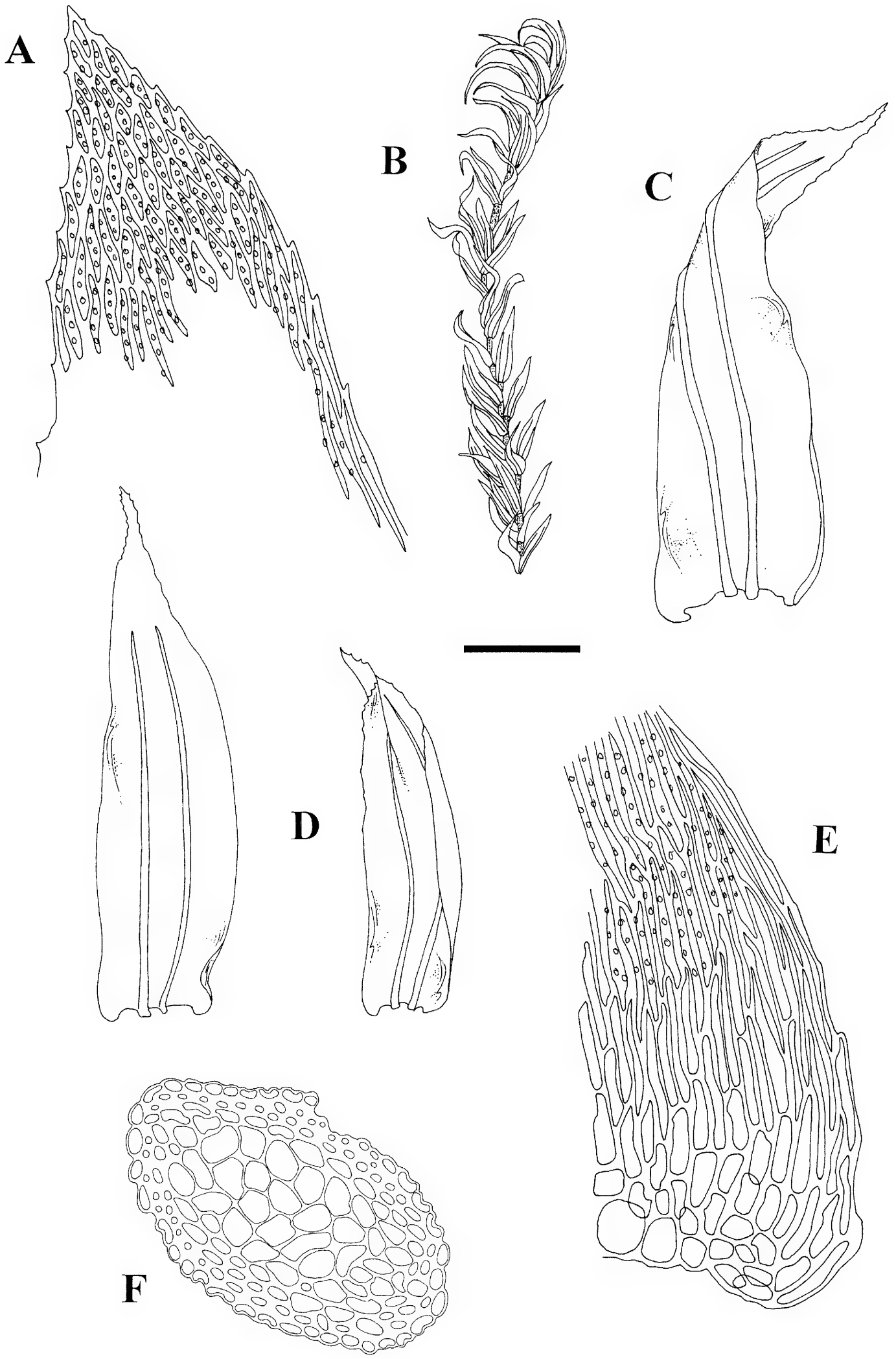


Figure 184. *Hypnella punctata*. A. Leaf apex. B. Habit. C & D. Leaves. E. Basal and alar cells. F. Stem in cross section. Scale in mm: bar = 0.04 (A, E); bar = 0.08 (F); bar = 0.23 (C, D); bar = 1.3 (B). All figure parts from *Glaziou* (type).

sclerodermis of 2–3 rows of small, thick-walled cells, enlarged cortical cells, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, at the base of the costae, and around branch primordia, smooth, reddish brown, not or sparsely and irregularly branched. Lateral leaves wide-spreading, more or less asymmetric, broadly ovate, oblong-ovate, oblong, or oblong-lanceolate, slenderly long-acuminate, flat or somewhat concave; margins serrulate above, entire below, plane or narrowly recurved, often broadly incurved on one side at base, not or obscurely bordered by 1–2 rows of long, narrow cells; costae double, ending at or just above midleaf, slender, diverging throughout, smooth, not projecting at the tips; cells smooth, apical cells broadly rhomboidal to elongate-rhomboidal, lower cells more elongate and narrower; basal cells enlarged, more or less bulging, cells across the insertions enlarged, short-rectangular, in 1–2 rows; alar cells not differentiated. Dorsal and ventral leaves erect, symmetric. Asexual reproduction at times by gemmae. Dioicous, autoicous, or synoicous. Setae elongate, smooth or papillose. Capsules erect to inclined, oblong or oblong-cylindric, neck well developed; exothecial cells oblong to subrectangular, collenchymatous; stomata fully formed, 2-celled, on neck; opercula conic-rostrate; annuli massive, of 5–7 rows of thin-walled, quadrate cells, separating from capsule along dehiscent zone at base, persistent on the operculum; peristome diplolepideous; exostome teeth narrowly triangular, dark red, median furrows present, dorsal trabeculae projecting laterally, densely and closely striate below, coarsely papillose above, ventral surface yellowish, deposition thin, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not or faintly perforate, cilia absent. Calyptrae mitrate, reddish to yellowish white, irregularly lobed at base, smooth or hairy.

Lepidopilidium is a genus of 29 species (Crosby *et al.* 2000). There is one *Lepidopilidium* species reported from Sri Lanka, but otherwise it is restricted to the tropical and south temperate regions of the New World and Africa. The centers of distribution for *Lepidopilidium* appear to be Brazil (11 species) and the Mascarene Islands (9 species). However, the genus has been grossly over-described, and the actual species number as well as the application of names within the genus remain uncertain.

Plants of *Lepidopilidium* are medium-sized, and they can be green, yellowish green, or reddish in color. Its stems have a distinct hyalodermis and pseudoparaphyllia are absent. The plants are moderately to strongly complanate-foliate, and as a result the leaves are more or less dimorphic: lateral leaves long, narrow, asymmetric; dorsal and ventral leaves short, broad, symmetric. The leaves have narrowly acuminate apices, serrulate upper leaf margins that are not to weakly bordered, and slender, double costae that are smooth at back and do not project at the tips. The leaf cells are smooth and broadly rhomboidal to elongate-rhomboidal in the upper parts of the leaf. Some species have uniseriate, multicellular gemmae clustered abaxially to the leaf insertions opposite the costae in the same position as the rhizoidal initials. The setae in *Lepidopilidium* can be smooth or papillose, and the capsules are distinctive in having a massive, persistent annulus consisting of 5–7 rows of hyaline to yellowish, thin-walled hexagonal cells. Unlike in most other members of the Hookeriaceae, the stomata have two fully formed subsidiary cells. *Lepidopilidium* has a typical hookeriaceous peristome. The calyptrae are mitrate, irregularly fringed at base, and sometimes sparsely hairy.

Lepidopilidium is nearly gametophytically identical to *Lepidopilum*, and without familiarity with the individual species the two genera are indistinguishable on the basis of their gametophytes. *Lepidopilum* differs fundamentally from *Lepidopilidium* in having a daltoniaceous rather than hookeriaceous peristome. In addition, some species of *Lepidopilum* have spinose setae and calyptrae with multiseriate ramenta; these features are lacking in *Lepidopilidium* and can be used to separate the two genera.

Despite its remarkable gametophytic similarity to *Lepidopilum*, *Lepidopilidium* appears more closely related to *Thamniopsis* on the basis of its hookeriaceous peristome, massive, persistent annulus, lax leaf areolation, and stems that have a well-developed hyalodermis. As presently circumscribed, *Thamniopsis* is a large, unwieldy genus in need of revision. Some *Thamniopsis* species are abundantly distinct from *Lepidopilidium*, but the genus encompasses so much variation that it is difficult to technically separate the two genera. In fact, the only feature of *Lepidopilidium* not found in at least one species of *Thamniopsis* is the presence of stomata with two fully formed subsidiary cells.

The name *Lepidopilidium* combines the generic name *Lepidopilum* with the Greek substantival suffix *-idium* (indicating diminutive).

1. Setae papillose, 4–5 mm long; leaves 1.7–3.0 mm long; gemmae absent; plants autoicous or synoicous. . . . . 1. *L. divaricatum*
1. Setae smooth, 5–15 mm long; leaves 1.0–2.5 mm long; gemmae often present; plants dioicous . . . . . 2. *L. portoricense*

1. *Lepidopilidium divaricatum* (Dozy & Molk.) Broth., Nat. Pflanzenfam. I(3): 944. 1907. *Hookeria divaricata* Dozy & Molk., Prodr. Fl. Bryol. Surinam. 49. 1854. *Lepidopilum divaricatum* (Dozy & Molk.) Mitt., J. Linn. Soc., Bot. 12: 379. 1869. Protologue. In Venezuela, juxta Rio Catuche, ubi collegit, *P. W. Korthals*.

Lepidopilum subdivaricatum Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32(1): 195. 1894. *Lepidopilidium subdivaricatum* (Renauld & Cardot) Broth., Nat. Pflanzenfam. I(3): 944. 1907. Protologue: [Costa Rica] Sine loco (*Pitt. N° 5658*). Type. Costa Rica. *Sine loco* (*Pitt*[*ier*] *n° 5658* (FH, isotype), *syn nov.*

Lepidopilidium synoicum Herzog, Biblioth. Bot. 87: 134. 1916. Protologue. [Bolivia] An feuchten Steinen in der Quebrada de Pocona, ca. 2800 m, [*Herzog*] *No. 5140*. Type. Quebrada de Pocona, *Herzog 5140* (L, isotype).

Plants medium-sized, 2–3 cm long, green, yellowish green, or golden reddish, in lax mats. Stems prostrate, irregularly branched, complanate-foliate, hyaline to yellowish when young, becoming reddish with age; stems in cross section with hyalodermis, subepidermal sclerodermis of 2–3 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, at the base of the costae, and around branch primordia, smooth, reddish brown, not or sparsely and irregularly branched. Leaves dimorphic. Lateral leaves wide-spreading, more or less asymmetric, broadly ovate, oblong-ovate, oblong, or oblong-lanceolate, 1.7–3.0 mm long, slenderly long-acuminate, flat or somewhat concave; margins serrulate above, entire below, plane, often broadly incurved on one side at base, not or obscurely bordered by 1–2 rows of long, narrow cells; costae double, ending at or just above midleaf, slender, diverging throughout, smooth, not projecting at the tips; cells smooth, apical cells broadly rhomboidal to elongate-rhomboidal, 60–100 × 10–20 µm, lower cells more elongate and narrower; basal cells enlarged, more or less bulging, cells across the insertions enlarged, short-rectangular, in 1–2 rows; alar cells not differentiated. Dorsal and ventral leaves erect, symmetric. Asexual gemmae absent. Autoicous or synoicous. Setae elongate, 3–5 mm long, yellow when young, becoming orange or red when old, papillose throughout. Capsules erect to inclined, oblong, 1 mm long, neck well developed; exothecial cells at mouth quadrate, in 1–3 rows, those below oblong to subrectangular, collenchymatous; stomata fully formed, 2-celled, on neck; opercula conic-rostrate, 0.7 mm long; annuli massive, of 5–7 rows of thin-walled, quadrate cells, separating from capsule along dehiscent zone at base, persistent on the operculum; peristome diplolepideous; exostome teeth narrowly triangular, dark red, with well-developed, pale yellow median furrows, dorsal trabeculae projecting laterally, densely and closely striate below, coarsely papillose above, ventral surface yellowish, deposition thin, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not or faintly perforate, cilia absent. Spores rounded, 12–20 µm, smooth to faintly papillose. Calyptrae mitrate, reddish to yellowish white, irregularly lobed at base, smooth, 1.5 mm long.

Illustrations. Dozy and Molkenboer (1854, Pl. 13); Welch (1971b, Figs. 173–181); Gradstein *et al.* (2001, Fig. 168 A–C). Figure 185.

Habitat. On bark of trees; 1850–2200 m.

Distribution in Central America. HONDURAS. Comayagua: *Allen 12308* (MO); Ocotepeque: *Allen 14488* (MO, TEFH). COSTA RICA. Sine loco. *Pittier 5658* (FH). PANAMA. Chiriquí: *Salazar 5749a* (MO).

World range: Mexico; Central America; Western, Northern, and Southern South America.

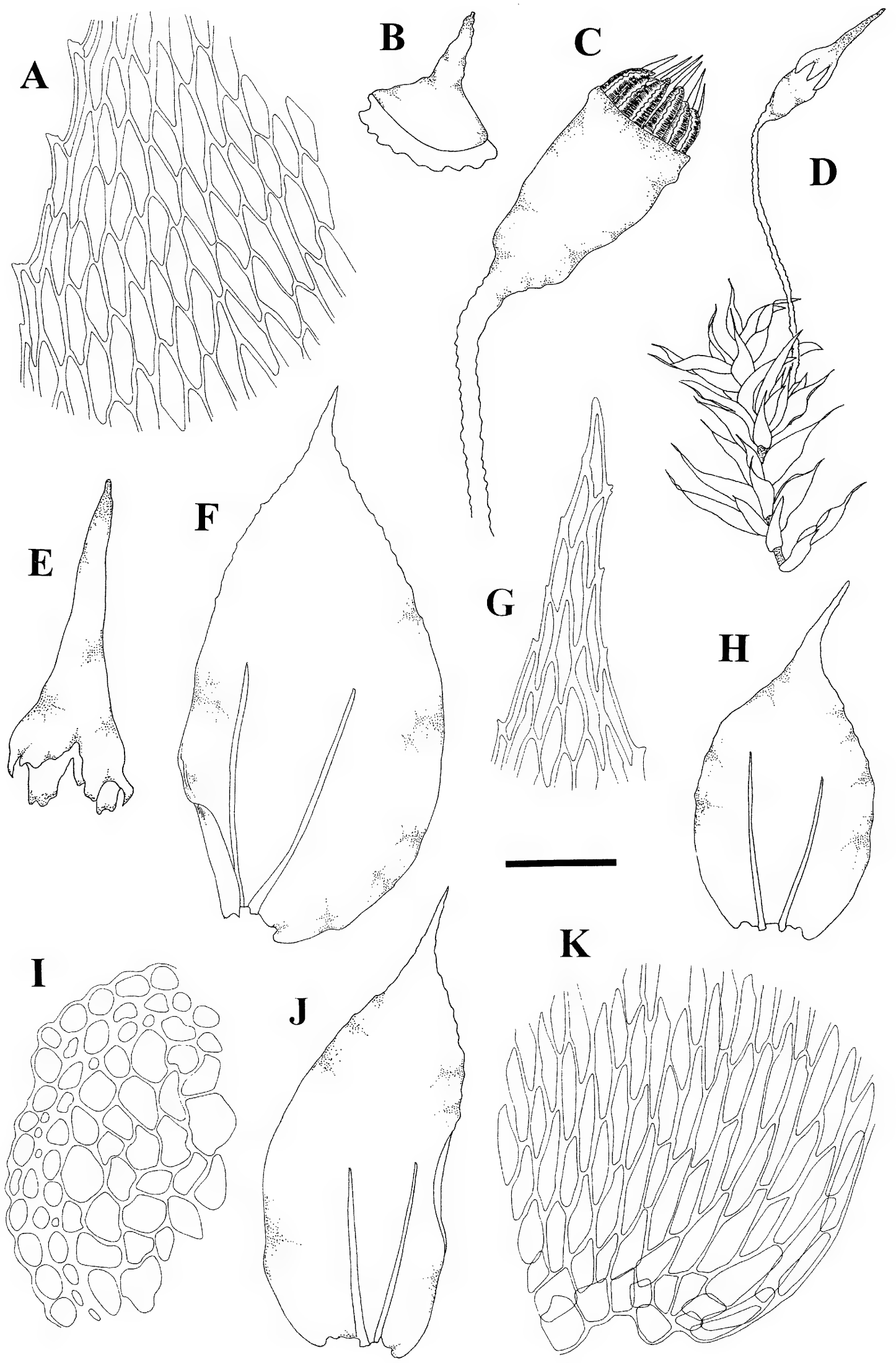
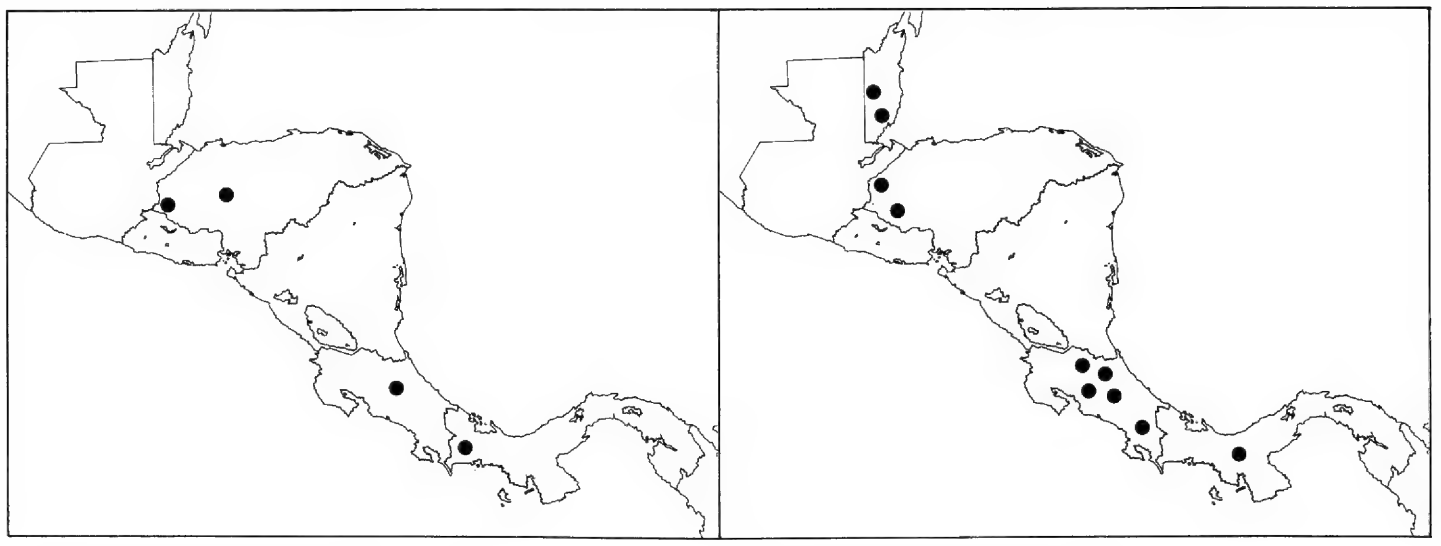


Figure 185. *Lepidopilidium divaricatum*. A. Median leaf cells and margin. B. Operculum and annulus. C. Seta and capsule. D. Habit. E. Calyptra. F & J. Lateral leaves. G. Leaf apex. H. Ventral leaf. I. Stem in cross section. K. Basal and alar cells. Scale in mm: bar = 0.08 (A, G, I, K); bar = 0.5 (B, C, E, F, H, J); bar = 1.56 (D). B–E, H, J from *Allen 12308*; all other figure parts from *Allen 14488*.



Lepidopilidium divaricatum *Lepidopilidium portoricense*

Lepidopilidium divaricatum is a medium-sized species with complanate-foliate plants. Due to its complanate habit, the leaves are dimorphic, with asymmetric lateral leaves and symmetric ventral and dorsal leaves. The lateral leaves tend to be longer and narrower than the ventral and dorsal leaves, and they often have one basal margin broadly inflexed. The leaves vary from broadly ovate to oblong or oblong-lanceolate, and they have long, narrowly acuminate apices, serrulate upper leaf margins that are sometimes obscurely bordered by long, narrow cells, and weak, smooth costae that do not project at the tips. The leaf cells are smooth, with broad, rhomboidal to elongate-rhomboidal upper cells. *Lepidopilidium divaricatum* is autoicous or synoicous and sporophytes are often encountered. The setae in *L. divaricatum* are short and papillose throughout. Its capsules have a massive annulus that consists of 5–7 rows of thin-walled, quadrate cells that separate from the capsule along a dehiscent zone at base and are persistent on the operculum. The stomata have two fully formed subsidiary cells. The exothecial cells are collenchymatous, and there is a hookeriaceous peristome with well-developed median furrows. The calyptrae are mitrate, lobed at base, papillose-roughened above, and naked.

In Central America *Lepidopilidium portoricense* is gametophytically very similar to *L. divaricatum*. The leaves of *L. portoricense* are a little bit smaller than those of *L. divaricatum*, but otherwise the gametophytes of *L. portoricense* differ from those of *L. divaricatum* only in sexual condition (dioicous vs. autoicous or synoicous), in having clusters of uniseriate, multicellular gemmae abaxial to the leaf insertions opposite the costae, and in having sparsely hairy calyptrae. Their sporophytes, however, are distinctly different, with *L. portoricense* having longer (7–13 mm vs. 3–5 mm), smooth setae and exostome teeth with weakly developed median furrows.

2. *Lepidopilidium portoricense* (Müll. Hal.) H. A. Crum & Steere, Bryologist 59: 253. 1956. *Crossomitrium portoricense* Müll. Hal., Hedwigia 37: 244. 1898. *Lepidopilum portoricense* (Müll. Hal.) Broth., Nat. Pflanzenfam. I(3): 957. 1907. Protologue. Portorico, prope Aybonito, ad arbores sylvae primaevae montis Cuyon, Nov. 1885: *P. Sintenis* in Hb. Krug et Urban.

Hookeria tenuiseta Müll. Hal., Hedwigia 39: 272. 1900. *Lepidopilidium tenuisetum* (Müll. Hal.) Broth., Nat. Pflanzenfam. I(3): 944. 1907. Protologue. Brasilia, Sa. Catharina, colonia Blumenau, ad trunculum arboris sylvestris prope rivulum Mulde, Julio 1888: *E. Ule*, Coll. *No.* 317; Joinville, in sylva primaeva, Junio 1888, sterilis: idem, *No. 468.*

Plants medium-sized, 2–4 cm long, green, yellowish green, golden or reddish, in dense or lax mats. Stems prostrate, irregularly branched, complanate-foliate, hyaline to yellowish when young, becoming reddish with age; stems in cross section with hyalodermis, subepidermal sclerodermis of 2–3 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, at the base of the costae, and around branch primordia, smooth, reddish brown, not or

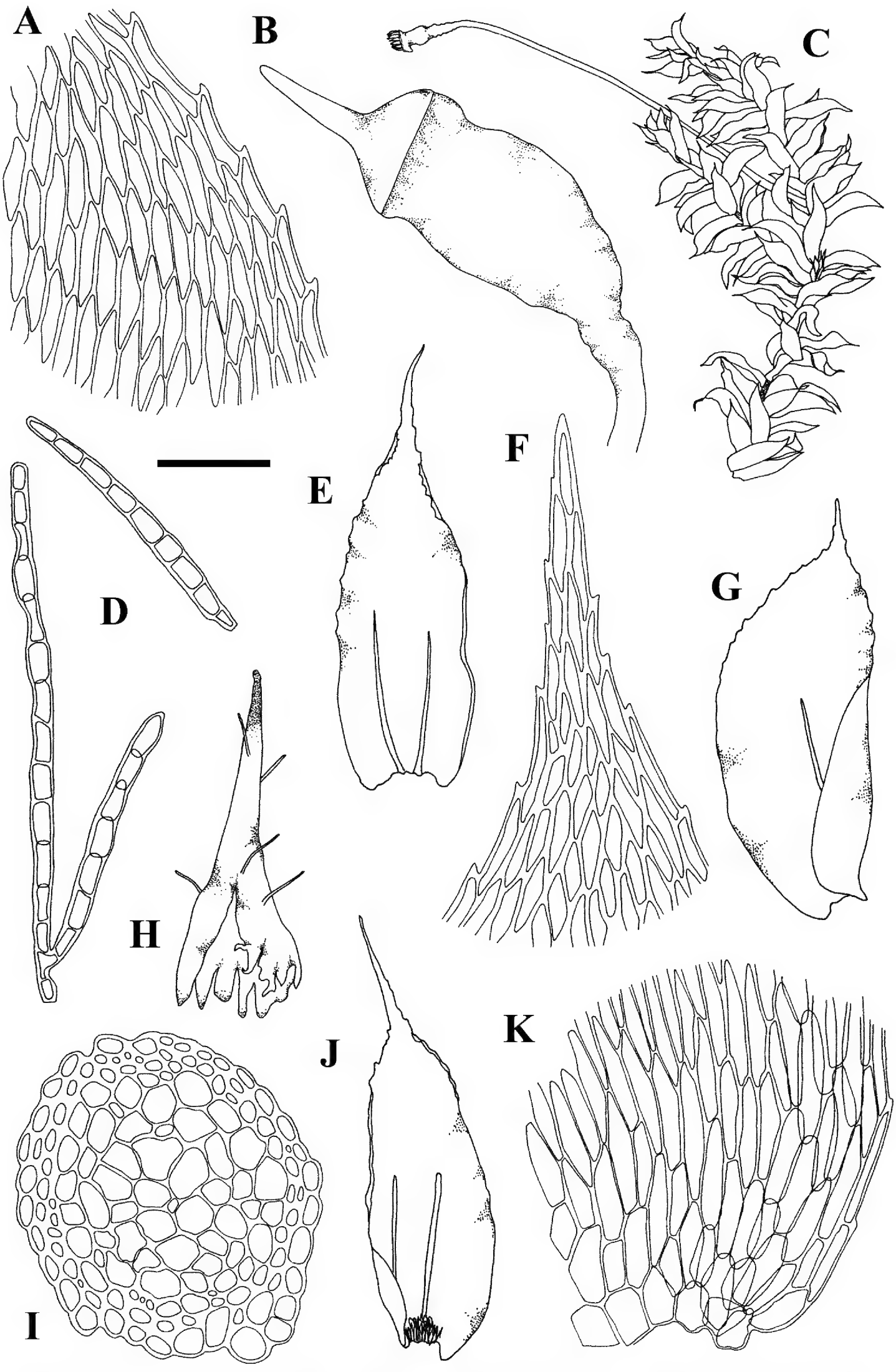


Figure 186. *Lepidopilidium portoricense*. A. Median leaf cells and margin. B. Seta, capsule, and operculum. C. Habit. D. Gemmae. E & J. Dorsal leaves. F. Leaf apex. G. Lateral leaf. H. Calyptra. I. Stem in cross section. K. Basal and alar cells. Scale in mm: bar = 0.08 (A, F, I, K); bar = 0.13 (D); bar = 0.5 (E, G, J); bar = 0.6 (B, H); bar = 2.5 (C). D, E, J from *Allen 19014*; all other figure parts from *Allen 18955*.

sparsely and irregularly branched. Leaves dimorphic. Lateral leaves wide-spreading, more or less asymmetric, broadly ovate, oblong-ovate, oblong, or oblong-lanceolate, 1.0–2.5 mm long, flat or somewhat concave, slenderly long-acuminate; margins serrulate above, entire below, plane or narrowly recurved, often broadly incurved on one side at base, not or obscurely bordered by 1–2 rows of long, narrow cells; costae double, ending 1/2–2/3 the leaf length, thin, diverging throughout, smooth, not projecting at tips; cells smooth, apical cells rhomboidal to elongate-rhomboidal, 40–90 × 10–16 µm, lower cells more elongate and narrower; basal cells enlarged, more or less bulging, cells across the insertions enlarged, short-rectangular, in 1–2 rows; alar cells not differentiated. Dorsal and ventral leaves erect, symmetric. Asexual reproduction often by gemmae clustered abaxially to the leaf insertions opposite the costae, in same position as the rhizoidal initials; gemmae uniseriate, multicellular. Dioicous. Setae elongate, 7–13 mm long, yellow when young, becoming orange or red when old, smooth throughout. Capsules erect to inclined, oblong-cylindric, 1.5–2.0 mm long, neck well developed; exothecial cells at mouth quadrate, in 1–3 rows, those below oblong to subrectangular, collenchymatous; stomata fully formed, 2-celled, on neck; opercula long conic-rostrate, 1.0 mm long; annuli massive, of 5–7 rows of thin-walled, quadrate cells, separating from capsule along dehiscent zone at base, persistent on the operculum; peristome diplolepideous; exostome teeth narrowly triangular, dark red, with narrow, pale yellow median furrows, dorsal trabeculae projecting laterally, densely and closely striate below, coarsely papillose above, ventral surface yellowish, deposition thin, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not or faintly perforate, cilia absent. Spores rounded, 14–22 µm, smooth to faintly papillose. Calyptrae mitrate, reddish to yellowish white, irregularly lobed at base, sparsely hairy or smooth, 2 mm long.

Illustrations. Welch (1969, Figs. 164–168); Florschütz-de Waard (1986, Fig. 130); Sharp *et al.* (1994, Fig. 616); Duarte Bello (1997, Pl. 249); Buck (1998, Pl. 16 1–8); Buck (2003, Fig. 91). Figure 186.

Habitat. On trunks of trees and tree ferns, leaves, roots, and rotting logs; 700–1720 m.

Distribution in Central America. BELIZE. Cayo: *Allen 15047* (MO); Toledo: *Allen 18955* (BRH, MO). HONDURAS. Copán: *Allen 17729* (MO, TEFH); Lempira: *Allen 11216* (MO, NY, TEFH). COSTA RICA. Alajuela: *Brenes* (NY); Cartago: *Crosby & Crosby 8578* (MO); Heredia: *Crosby 13120* (MO); Puntarenas: *James 1969-80* (US); San José: *Standley 42431b* (FH, US). PANAMA. Veraguas: *Crosby 10194* (MO).

World range: Mexico; Central America; Caribbean; Northern South America, Brazil.

Lepidopilidium portoricense is a medium-sized species with complanate-foliate plants. It exhibits a large degree of leaf variability. The variable nature of its leaves is partly due to the presence of dimorphic leaves: asymmetric lateral leaves; symmetric ventral and dorsal leaves. Plants also vary considerably between populations, and this variability appears to be habitat related. Collections made from tree trunks or logs have relatively short, broad leaves with mostly plane margins. Plants growing on leaves are more attenuate and have longer, narrower leaves that are often erect or narrowly recurved at the margins. The leaves vary from broadly ovate to oblong or oblong-lanceolate, and they have long, narrowly acuminate apices, serrulate upper leaf margins, and weak, smooth costae that do not project at the tips. The leaf cells are smooth, with rather broad, rhomboidal to elongate-rhomboidal upper cells. A distinctive feature of *L. portoricense* is the presence of clusters of uniseriate, multicellular gemmae that arise from initials abaxial to the leaf insertions opposite the costae. The gemmae initials occur in the same position as the rhizoidal initials.

Lepidopilidium portoricense is dioicous, but sporophytes are often encountered. The setae in *L. portoricense* are smooth and relatively long for the genus. Its capsules have a massive annulus that consists of 5–7 rows of thin-walled, quadrate cells that separate from the capsule along a dehiscent zone at base and are persistent on the operculum. The stomata have two fully formed subsidiary cells. The exothecial cells are collenchymatous, and it has a hookeriaceous peristome with weakly developed median furrows. The calyptrae are mitrate, lobed at base, and usually sparsely hairy.

In Central America *Lepidopilidium divaricatum* differs gametophytically from *L. portoricense* only in its autoicous sexual condition and its lack of gemmae. Their sporophytes, however, are dis-

tinctly different, with *L. divaricatum* having shorter setae (4–5 mm vs. 7–13 mm) that are densely papillose rather than smooth, and exostome teeth with well-developed median furrows.

The *scabrisetum*-group of *Lepidopilum* is nearly gametophytically identical to *Lepidopilidium portoricense*. Although the leaves of *Lepidopilum* never have the narrowly recurved upper margins sometimes seen in *Lepidopilidium*, unless one is familiar with the individual species the two genera are indistinguishable on the basis of their gametophytes. *Lepidopilum* differs fundamentally in having a daltoniaceous rather than a hookeriaceous peristome, and many of its species have densely papillose to spinose setae. In addition, the calyptrae in *Lepidopilum* often have numerous multicellular ramenta.

Buck (1998) placed the south Brazilian *Lepidopilidium tenuisetum* into synonymy with *L. portoricense* and suggested the name *portoricense* may eventually be replaced after the genus is more thoroughly evaluated. In this regard, there are notes accompanying specimens in the MO herbarium that indicate *L. portoricense* is the same as *L. nitens* (Hornsch.) Broth. *Lepidopilidium nitens* predates *L. portoricense* by 58 years.

11. *Lepidopilum* (Brid.) Brid., Bryol. Univ. 2: 267. 1827, conserved name. *Pilotrichum* P. Beauv. sect. *Lepidopilum* Brid., Muscol. Recent. Suppl. 4: 141. 1819. *Hookeria* Sm. sect. *Lepidopilum* (Brid.) Müll. Hal., Syn. Musc. Frond. 2: 192. 1851.

Plants small, medium-sized, or robust, glossy or dull, glaucous green, green, dark green, yellowish green, yellow or yellowish red, or reddish, in loose tufts or dense mats. Primary stems prostrate and creeping. Secondary stems prostrate or ascending, sometimes pendent, not or sparsely branched; stems and branches at times filiform-attenuate, in cross section with hyalodermis (absent in *L. ultramarginatum*), 1–5 layers of small, thick-walled subepidermal cells, enlarged, thin-walled cortical cells, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong, hyaline; rhizoids on primary stems and secondary stems, from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, sparsely and irregularly branched or pinnately branched. Leaves closely or distantly spaced, complanate or evenly foliate, often dimorphic, erect-spreading, spreading, or falcate-spreading, smooth or undulate when wet, smooth, undulate, flexuose-contorted, crispate when dry, lanceolate, ovate-lanceolate, oblong-lanceolate, broadly ovate, ovate-oblong, oval-oblong, oblong, obovate, spathulate, oblong-lingulate, or lingulate, symmetric or asymmetric, obtuse, acute, short-acuminate or long-acuminate, at times apiculate; margins plane, erect, or revolute, often broadly infolded on one side at base, upper margins entire, subentire, serrulate, serrate, or spinose, bordered or elimbate; costae double, usually weak, occasionally strong, at times one fork or both fused to the leaf border, smooth at back, usually not projecting at the apices; cells smooth, median cells hexagonal, oblong-hexagonal, rhomboidal, narrowly to broadly fusiform, long-fusiform, or linear-fusiform, thin- or firm-walled, porose or not porose, lower cells broadly fusiform, elongate-rhomboidal, rectangular, oblong-rectangular, elongate-rectangular, thin- or firm-walled, porose or not porose, cells across the base enlarged, subrectangular; alar cells not differentiated. Asexual propagula often present, fusiform, multicellular, uniseriate, arising from clusters of initials abaxial to the leaf insertions at base of costae, occasionally arising at the tips of the leaves and along the leaf margins. Autoicous, synoicous, or dioicous. Setae elongate or short, red to reddish orange, usually papillose or spiculose throughout, occasionally weakly papillose above and smooth below. Capsules erect, ovoid to oblong-cylindrical, neck well developed; exothecial cells reddish, oblate at mouth, those below rounded, oblong, to rectangular, thick-walled, not, somewhat, or strongly collenchymatous; stomata rudimentary, 3–6-celled, on neck; opercula high-conic; annuli of numerous rows of thin-walled cells, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome very narrowly triangular, median furrow absent, dorsal (outer) surface broad, whitish yellow, lightly papillose throughout, trabeculae thin, median lines faint, ventral (inner) surface narrow, 1/3 or less the width of the dorsal surface, red or yellow, lightly papillose, deposition thick; endostome as long as the exostome, pale yellowish, papillose throughout, basal membranes high, segments broad, concave-keeled, not perforate, cilia absent. Calyptrae campanulate-mitrate, irregularly lobed at base, scabrous, usually with multicellular ramenta, occasionally naked.

Lepidopilum is a tropical genus of 30 species. Two of its species are restricted to the Paleotropics (Central Africa and Madagascar), and the other 28 species are Neotropical in distribution: southern Mexico to Argentina and Brazil. Although Central America has 18 *Lepidopilum* species, the center of distribution for the genus appears to be in Ecuador. *Lepidopilum* is a taxonomically difficult genus because it exhibits considerable morphological variability. Its plants can be slender, medium-sized, or robust, and they vary in color from glaucous green, green, yellowish, to reddish. *Lepidopilum* stems always have a distinct hyalodermis, but leaf stance varies from strongly complanate-foliate to evenly foliate. Many species of *Lepidopilum* have sparse and irregularly branched rhizoids, but others have dense and pinnately branched rhizoids. The leaves in *Lepidopilum* have a broad array of forms from lanceolate to spathulate or lingulate. They can be symmetric or strongly asymmetric, and variously dimorphic or monomorphic, with apices varying from obtuse, apiculate, acute, short-acuminate, to long-acuminate. The leaf margins can be strongly bordered, weakly bordered, or elimbate; they can be entire, subentire, serrulate, serrate, or spinose. The costae in *Lepidopilum* usually end near midleaf and diverge throughout. They are typically weakly developed and smooth at back; they only rarely project at the tips. The leaf cells in *Lepidopilum* are smooth, and they vary from broadly hexagonal to linear-fusiform. They can be thin- or firm-walled, narrow or broad, and sometimes porose. The genus often reproduces asexually by means of hyaline or brown, fusiform, multicellular, uniseriate propagula that arise from clusters of initials abaxial to the leaf insertions at the base of the costae. Propagula are also occasionally produced at the tips of the leaves or along the leaf margins. Two species of *Lepidopilum* (*L. muelleri* and *L. scabrisetum*) reproduce asexually by means of deciduous leaves. Many species of *Lepidopilum* are autoicous or synoicous, and sporophytes are often encountered. *Lepidopilum* has long-conic opercula that can be more or less the same size as its capsules. The setae can be short or long, and in most species they are densely papillose to spinose. Although a few species of *Lepidopilum* have setae that are weakly papillose above and smooth below, entirely smooth setae are unknown in the genus. All species of *Lepidopilum* have the same massive (to 25 rows of cells high), persistent annulus that also characterizes the genus *Thamniopsis*. The capsules have rudimentary stomata consisting of 3–6 cells, and a daltoniaceous peristome. The calyptrae are campanulate-mitrate and irregularly lobed at base, and they usually have many multicellular hairs.

In Central America *Lepidopilum* can be confused with *Stenodesmus*, *Actinodontium*, *Crossomitrium*, *Stenodictyon*, or *Lepidopilidium*. *Stenodesmus*, *Actinodontium*, *Crossomitrium*, and *Lepidopilum* have identical daltoniaceous peristomes, as well as stems with a hyalodermis. The gametophytes of *Stenodesmus* and *Actinodontium* have evenly foliate stems with symmetric, elimbate leaves, which separate them from the majority of *Lepidopilum* species, which have complanate-foliate stems with asymmetric, bordered leaves. Nevertheless, there are some *Lepidopilum* species (*e.g.*, *Lepidopilum longifolium*) that have evenly foliate stems and symmetric, elimbate leaves. *Stenodesmus* is also similar to *Lepidopilum* in having spinose setae; however, its leaves are abruptly constricted above into long, narrow apices, and this feature distinguishes it from all species of *Lepidopilum*. This sole distinguishing feature of *Stenodesmus* is not enough to warrant the recognition of two genera, but whether the genera should be synonymized or the *Stenodesmus*-like members of *Lepidopilum* transferred to *Stenodesmus* is debatable. *Actinodontium* differs from *Lepidopilum* in having smooth setae, but gametophytically it is nearly identical to the *longifolium*-group of *Lepidopilum*. The gametophytes of *Actinodontium* can be distinguished from *Lepidopilum* only in having naked calyptrae and leaves with shorter, more broadly acuminate apices, more strongly recurved leaf margins, and somewhat longer costae. *Crossomitrium* is gametophytically similar to *Lepidopilum* in leaf form and areolation. Both genera also are often epiphytic or epiphyllous and commonly have propagula. *Crossomitrium* differs from *Lepidopilum* in having absolutely ecostate leaves.

Stenodictyon and *Lepidopilidium* differ essentially from *Lepidopilum* in having hookeriaceous peristomes. In addition, *Stenodictyon* also has smooth setae, and, although its leaves are somewhat similar to those of the *longifolium*-group of *Lepidopilum* in shape, areolation, and costal form, they differ consistently in being abruptly narrowed above into hair-points. *Lepidopilidium* is nearly gametophytically identical to the *scabrisetum*-group of *Lepidopilum.* Although the leaves of *Lepidopilidium* differ from those of *Lepidopilum* in sometimes having narrowly recurved upper margins, unless one is familiar with the individual species, the two genera are indistinguishable on the basis of their gametophytes. In addition to their peristome differences, *Lepidopilidium* differs from *Lepidopilum* in having smooth setae and calyptrae that are naked or sparsely hairy.

Lepidopilum was revised by Churchill (1988) in an unpublished doctoral dissertation that included many new synonyms and lectotypifications, but no new species.

The name *Lepidopilum* combines the Greek *lepidos* (scale) with *pilos* (hair or felt), and it refers to the multicellular hairs on its calyptrae.

1. Lateral leaves limbate, with 1–14 rows of linear cells; inner laminal cells broadly rhomboidal-fusiform, rhomboidal, or hexagonal 2
1. Lateral leaves elimbate or inconspicuously limbate; inner laminal cells similar to marginal cells or gradually grading into marginal cells 11

2. Plants lax; leaves broadly obovate to oval; upper cells laxly bulging, 130–150 × 30–55 µm; margins entire to serrulate . . . . . 6. *L. diaphanum*
2. Plants stiff; leaves obovate, ovate-lanceolate, ovate, ovate-oblong, or oblong-lanceolate; upper leaf cells firm, 33–144 × 15–55 µm; margins serrulate, serrate to spinose. 3

3. Lateral leaves long-acuminate, 3.5–8.0 mm long; setae 2–4 mm long . . . . . 13. *L. polytrichoides*
3. Lateral leaves apiculate, short-acuminate, or long-acuminate, 1.8–5.0 mm long; setae short or long 4

4. Leaves short- or long-acuminate 5
4. Leaves apiculate or bluntly acute. 8

5. Leaves 4.0–5.0 mm long; margins often doubly serrate . . . . . 12. *L. permarginatum*
5. Leaves 1.8–3.5 mm long; margins uniserrate 6

6. Leaves bordered above by 4–8 rows of cells, border at base very strong, 10–14 rows of cells; one fork of costa often fused more or less throughout with margin; setae 10–12 mm long . . . . . 18. *L. ultramarginatum*
6. Leaves bordered above by 2–3 rows of cells, border at base weak, 1–2(–3) rows of cells; costae not or rarely merging with margins; setae 3–5 mm long. 7

7. Leaves 3.0–3.5 mm long, flexuose-contorted whether wet or dry; upper margins sharply serrate; costae strong throughout and often projecting at the tips . . . . . 8. *L. inflexum*
7. Leaves 1.8–2.2 mm long, flexuose-contorted when dry, flattened when wet; upper margins serrulate; costae slender, tapering and not projecting at tips. . . . . 7. *L. exiguum*

8. Leaves 2.0–3.2 mm long 9
8. Leaves 3–5 mm long 10

9. Leaves strongly crispate when dry, strongly bordered; costae 2/3–3/4 the leaf length; setae 10–12 mm long. . . . . 17. *L. tortifolium*
9. Leaves erect-twisted when dry, weakly bordered; costae 1/2 the leaf length; setae 2.5–3.0 mm long. . . . . 16. *L. surinamense*

10. Lateral leaves broadly ovate to ovate-oblong; costae ending near midleaf. . . . . 4. *L. curvifolium*
10. Lateral leaves oblong-lanceolate or oblong-lingulate; costae ending above midleaf . . . . . 15. *L. stillicidiorum*

11. Leaf apices obtuse-rounded, apiculate 12
11. Leaf apices acute, short-acuminate, or long-acuminate 13

12. Lateral leaves ovate-oblong to oblong-lingulate, undulate, not falcate; apices sharply serrate; stem tips not attenuate-foliate . . . . . 1. *L. affine*
12. Lateral leaves oblong to oblong-obovate, smooth, somewhat falcate; apices serrulate; stem tips often attenuate-foliate . . . . . 11. *L. pallidonitens*

13. Lateral leaves symmetric or nearly so, not falcate or falcate-sigmoid 14
13. Lateral leaves asymmetric, slightly to strongly falcate to falcate-sigmoid. 17

14. Leaves long-acuminate to piliferous 15
14. Leaves acute to short-acuminate 16

15. Leaves oblong-oval, oblong, or oblong-lanceolate; margins narrowly recurved in part or throughout, typically entire to serrulate; apices gradually and broadly acuminate, often reflexed-recurved when dry; upper leaf cells 10–17 µm wide . . . . . 9. *L. longifolium*
15. Leaves ovate-lanceolate or lanceolate; margins mostly plane, serrulate to sharply serrate; apices long, narrowly acuminate to piliferous, erect when dry; upper leaf cells 10–12 µm wide. . . . . 10. *L. muelleri*

16. Setae 5–13 mm long; capsules 1.5–2.0 mm long; rhizoids sparsely and irregularly branched; propagula on leaf bases and apices or along distal margins . . . . . 2. *L. amplirete*
16. Setae 2.5–3.0 mm long; capsules 1.5–2.5 mm long; rhizoids densely pinnately or bipinnately branched; propagula on leaf bases or in dense terminal clusters . . . . . 16. *L. surinamense*

17. Leaf apices long-acuminate 18
17. Leaves short-acuminate. 20

18. Leaves 2.5–4.0 mm long; setae 5–13 mm long . . . . . 10. *L. muelleri*
18. Leaves 2–3 mm long; setae 1.5–3.0 mm long 19

19. Calyptrae with many multicellular ramenta . . . . . 5. *L. cuspidans*
19. Calyptrae naked or with a few multicellular ramenta . . . . . 3. *L. brevipes*

20. Lateral leaves 2–4 mm long; deciduous leaves sometimes present; setae 5–9 mm long; calyptrae with many multicellular ramenta. . . . . 14. *L. scabrisetum*
20. Lateral leaves 2–3 mm long; deciduous leaves absent; setae 1.5–3.0 mm long; calyptrae naked or with a few multicellular ramenta . . . . . 3. *L. brevipes*

1. *Lepidopilum affine* Müll. Hal., Linnaea 21: 192. 1848. Protologue. [Suriname]. An Baumstämmen bei *Paramáribo*. Juni 1844 steril. Hb. *Kegel. No. 741.*

Lepidopilum antisanense E. B. Bartram, Rev. Bryol. Lichénol. 33: 11. 1964. Protologue. [Ecuador] On tree trunk to 30 ft., Shinguipino rain forest between Rio Napo and Tena, 8 km of Tena, c. 1500 ft., [*Peter J. Grubb*] *2925.* Types. Flora of Ecuador. Cerro Antisana (lat. 0°30′S : long. 78°W). On tree trunk to 30 ft., Shinguipuri rain forest between Rio Napo and Tena, 8 km S. E. of Tena, c. 1500 ft., 25.9.1960, *P. J. Grubb 2925* (FH, holotype; FH, isotype), *syn. nov.*

Plants medium-sized to robust, 2.0–2.5 cm long, glossy, light green to yellowish green, in dense mats. Primary stems prostrate and creeping. Secondary stems prostrate or weakly ascending, not or sparsely branched, hyaline to yellowish when young, becoming red to red brown with age, strongly complanate-foliate; stems in cross section with well-developed hyalodermis, 3–5 layers of small, thick-walled subepidermal cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong, hyaline; rhizoids on primary stems and secondary stems, from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves closely spaced, strongly flattened, weakly dimorphic. Lateral leaves erect-spreading to spreading when wet, spreading, undulate to crispate when dry, ovate-oblong to oblong-lingulate, 1.8–3.0 mm long, symmetric or weakly asymmetric, obtuse to broadly acuminate, apiculate; margins entire below, sharply serrate above, elimbate, plane above, broadly infolded on one side at base; costae double, weak, 1/4–1/3 the leaf length, diverging throughout, smooth at back, not projecting at the apex; cells smooth, median cells linear-fusiform to long-fusiform, 60–140 × 6–10 µm, thin-walled, not porose, lower cells elongate-rectangular, thin-walled, not porose, cells across the base enlarged, subrectangular; alar cells not differentiated. Dorsal leaves erect when wet, ovate-oblong to lingulate, 2 mm long, symmetric; margins entire below, sharply serrate above, elimbate, plane. Asexual propagula fusiform, multicellular, uniseriate, arising from clusters of initials abaxial to the leaf insertions at base of costae. Dioicous. Setae elongate, (6–)8–12 mm long, red to reddish orange, densely spiculose-papillose. Capsules erect, ovoid to oblong-cylindrical, 1.0–1.7 mm long, neck well developed and thickly tuberculate; exothecial cells reddish, oblate in 2–3 rows at mouth, those below rounded, oblong, to rectangular, thick-walled, somewhat collenchymatous; stomata rudimentary, 3–6-celled, on neck; opercula high-conic, 1.0 mm long; annuli of 10–20 rows of thin-walled

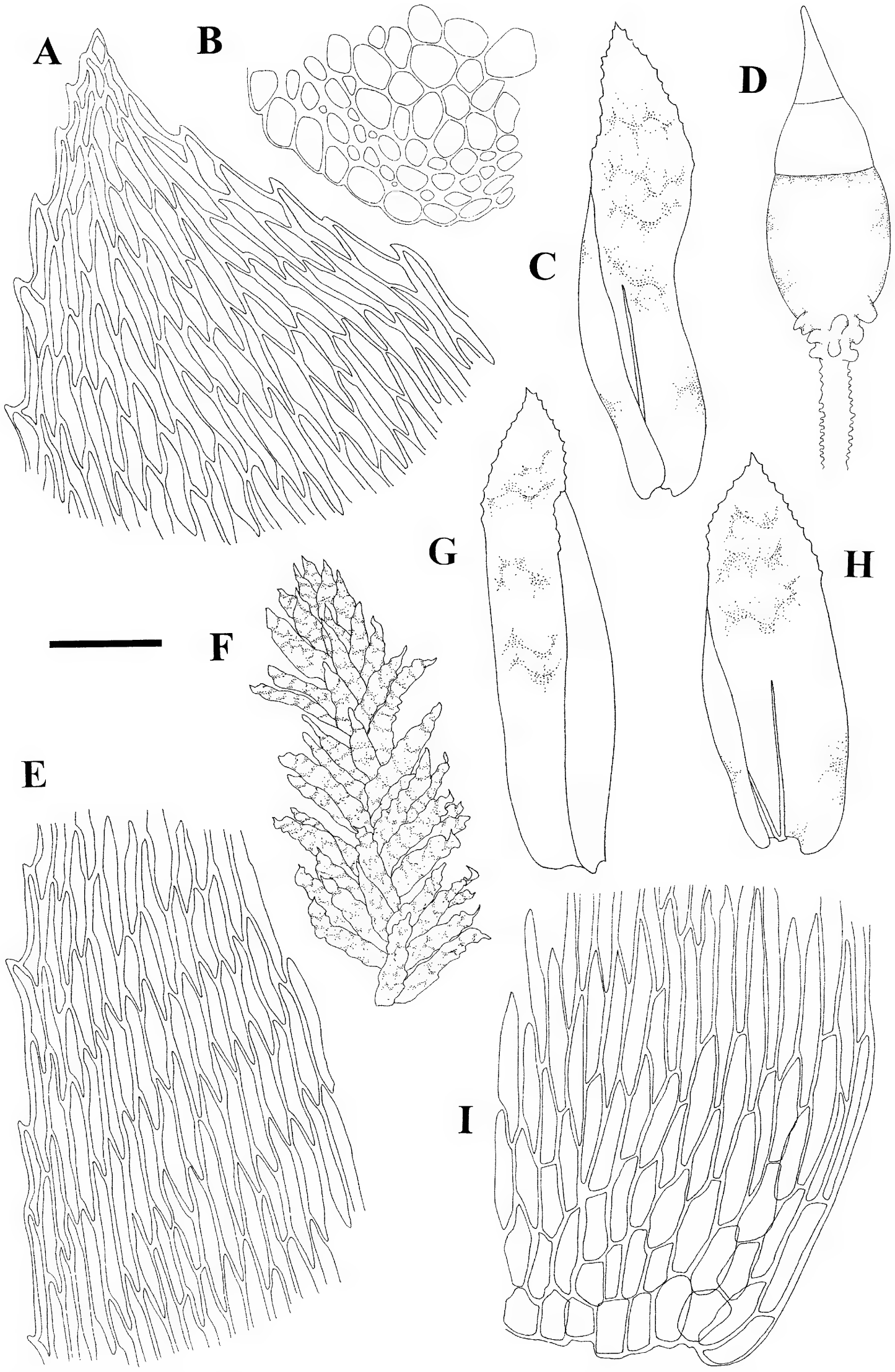
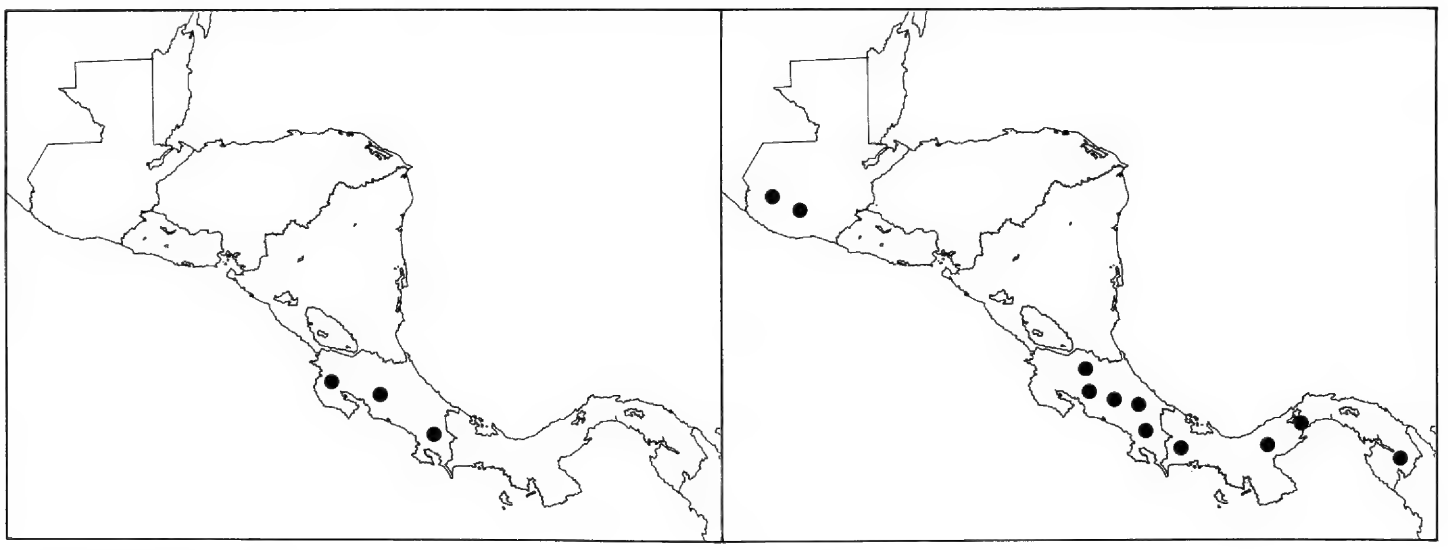


Figure 187. *Lepidopilum affine*. A. Leaf apex. B. Stem in cross section. C & G. Lateral leaves. D. Seta, capsule, annulus, and operculum. E. Median leaf cells and margin. F. Habit. H. Dorsal leaf. I. Basal and alar cells. Scale in mm: bar = 0.06 (A, B, E, I); bar = 0.5 (C, G, H); bar = 0.9 (D); bar = 1.96 (F). D from *van der Werff 15550*; all other figure parts from *Crosby 2607*.



Lepidopilum affine *Lepidopilum amplirete*

cells, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome very narrowly triangular, median furrow absent, dorsal (outer) surface broad, whitish yellow, lightly papillose throughout, trabeculae thin, median lines faint, ventral (inner) surface narrow, 1/3 or less the width of the dorsal surface, dark red, lightly papillose, deposition thick; endostome as long as the exostome, pale yellowish, papillose throughout, basal membranes high, segments broad, concave-keeled, not perforate, cilia absent. Spores rounded, 10–14 µm, smooth to lightly papillose. Calyptrae campanulate-mitrate, 1.2–2.0 mm long, reddish yellow, irregularly lobed at base, scabrous, with many multicellular ramenta.

Illustrations. Welch (1974, Figs. 371–384, as *L. pumilum*); Florschütz-de Waard (1986, Fig. 133); Churchill (1988, Figs. 30 & 31); Churchill (1994, Fig. 10 A–D). Figure 187.

Habitat. On tree trunks and lianas; near sea level to 1000 m.

Distribution in Central America. COSTA RICA. Guanacaste: *Alfaro* (FH); Puntarenas: *Koch 5050* (MO, NY, US); San José: *Crosby 2607* (MO).

World range: Central America; Western and Northern South America.

Lepidopilum affine is a medium-sized species with glossy, yellowish green plants that are flattened to the substrate and have strongly complanate-foliate stems. Central American collections have ovate-oblong to oblong-lingulate leaves that are distinctly undulate, but in South America (see Churchill 1988) some collections have smooth leaves. The leaves of *L. affine* have short, faint costae that end well below midleaf; unbordered, sharply serrate upper margins; and thin-walled, elongate-flexuose cells. Plants of *L. affine* are similar to some *Neckera* species in overall aspect as well as many technical features, but that genus has leaves with shorter costae, cucullate calyptrae, shorter, smooth setae, 2-celled stomata, rudimentary annuli, and a neckeraceous peristome with rudimentary endostomial cilia and exostome teeth cross-striate at base. *Lepidopilum affine* has long, spinose setae and capsules that are strongly tuberculate at base.

The flattened plants of *Lepidopilum affine* give it an aspect that in Central American species of *Lepidopilum* is also found in *L. muelleri*, *L. brevipes*, *L. scabrisetum*, *L. diaphanum*, and *L. pallidonitens.* All five species differ from *L. affine* in having smooth rather than undulate leaves. The first three species also differ in having acute or acuminate leaves with falcate to falcate-sigmoid lateral leaves. *Lepidopilum diaphanum* further differs in having bordered leaves with costae 1/2–2/3 the leaf length and very broad (30–50 µm wide) hexagonal to rhomboidal median leaf cells. *Lepidopilum pallidonitens* and *L. affine* both have rounded to obtuse leaf apices. However, *L. pallidonitens* has broadly oblong to oblong-obovate, falcate to falcate-sigmoid lateral leaves with serrulate upper margins. Plants of *L. pallidonitens* also differ from those of *L. affine* in often having attenuate-foliate branch and stem tips.

2. *Lepidopilum amplirete* (Sull.) Mitt., J. Linn. Soc., Bot. 12: 382. 1869. *Cylindrothecium amplirete* Sull., Proc. Amer. Acad. Arts 5: 284. 1861. *Entodon ampliretis* (Sull.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1876–77: 292. 1878. Protologue. [Cuba. *Charles Wright*] *72*. Rocky ledges in woods.

Hookeria cubensis Sull., Proc. Amer. Acad. Arts 5: 285. 1861. *Lepidopilum cubense* (Sull.) Mitt., J. Linn. Soc., Bot. 12: 384. 1869. Protologue. [Cuba. *Charles Wright*] *85*. On bushes in thick woods. Type. Plantae Cubenses Wrightianae. *85. Hookeria cubensis* (sp. nov.) Hab. On bushes in thick woods (FH, isotype).

Lepidopilum phyllorhizum Mitt., J. Linn. Soc., Bot. 12: 385. 1869. Protologue. Ins. Cuba, *Wright*, *n. 85*, ex parte.

Lepidopilum semilaeve Mitt., J. Linn. Soc., Bot. 12: 385. 1869. Protologue. [Panama] Hab. America centralis, Chargres, *Sinclair*. [Ecuador] Andes Quitenses, *Jameson*.

Lepidopilum apiculatum E. B. Bartram, J. Wash. Acad. Sci. 24(11): 477. 1934. Protologue. [Costa Rica] Banana River, 80 m, *F. Gutierrez*. Type. Plants of Costa Rica. Rio Banana, 80 m, May 17, 1934, *F. Gutierrez* (FH, holotype).

Lepidopilum skutchii E. B. Bartram, Bryologist 54: 239. 1951 [1952]. Protologue. [Costa Rica] Prov. San José: vicinity of El General, elev. 800–1100 m, *Alexander F. Skutch 2530* (type). Type. Plants of Costa Rica. Vicinity of El General, Prov. San José; alt. 1100 meters, *No. 2530 Alexander F. Skutch*, Collector, Jan. 1936 (FH, holotype; FH, MO, US, isotypes).

Plants medium-sized, 2–4 cm long, glossy, green to yellowish green, in loose tufts. Primary stems prostrate and creeping. Secondary stems ascending to erect, not or sparsely branched, hyaline to yellowish when young, becoming red to red brown with age; stems in cross section with well-developed hyalodermis, 3–5 layers of small, thick-walled subepidermal cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong, hyaline; rhizoids on primary stems and secondary stems, from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves closely or somewhat distantly spaced, weakly to not dimorphic, erect-spreading to spreading and flattened when wet, contorted to crispate when dry, oval-oblong, oblong, obovate, or spathulate, 1.5–3.0 mm long, symmetric, acute to short-acuminate, apiculate, apices often twisted whether wet or dry; margins sharply serrate, serrulate, or subentire above, entire below, elimbate or obscurely bordered by a row of elongate cells, plane or recurved below; costae double, 1/4–2/3 the leaf length, diverging throughout, smooth at back, at times projecting at the apices; cells smooth, median cells rhomboidal, fusiform, or oblong-hexagonal, 34–60 × 10–18 µm, thick-walled, sometimes porose, lower cells oblong-rectangular to elongate-fusiform, firm-walled, sometimes porose, cells across the base enlarged, subrectangular, yellow to reddish yellow; alar cells not differentiated. Asexual propagula fusiform, multicellular, uniseriate, arising at the tips of the leaves, along the leaf margins, or from clusters of initials abaxial to the leaf insertions at base of costae. Autoicous. Setae elongate, 5–13 mm long, red to reddish orange, smooth below, papillose above. Capsules erect, ovoid- to oblong-cylindrical, 1.5–2.0 mm long, neck well developed, papillose-roughened; exothecial cells reddish, oblate in 2–3 rows at mouth, those below rounded to oblong, to rectangular, thick-walled, strongly collenchymatous; stomata rudimentary, 3–5-celled, on neck; opercula high-conic, 1.0 mm long; annuli of 10–20 rows of thin-walled cells, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome very narrowly triangular, median furrow absent, dorsal (outer) surface broad, whitish yellow, lightly papillose throughout, trabeculae thin, median lines faint, ventral (inner) surface narrow, 1/3 or less the width of the dorsal surface, yellow, lightly papillose, deposition thick; endostome as long as the exostome, pale yellowish, papillose throughout, basal membranes high, segments broad, concave-keeled, not perforate, cilia absent. Spores rounded, 14–22 µm, smooth to lightly papillose. Calyptrae campanulate-mitrate, 2–3 mm long, reddish yellow, irregularly lobed at base, scabrous, with many multicellular ramenta.

Illustrations. Bartram (1934, Fig. 3); Bartram (1949, Fig. 138 D–F); Welch (1966, Figs. 186–198, as *L. cubense*); Welch (1969, Figs. 169–173); Welch (1974, Figs. 290–294, as *L. apiculatum*; Figs. 317–325, as *L. contiguum*; Figs. 394–404, as *L. semilaeve*; Figs. 405–417, as *L. skutchii*); Florschütz-

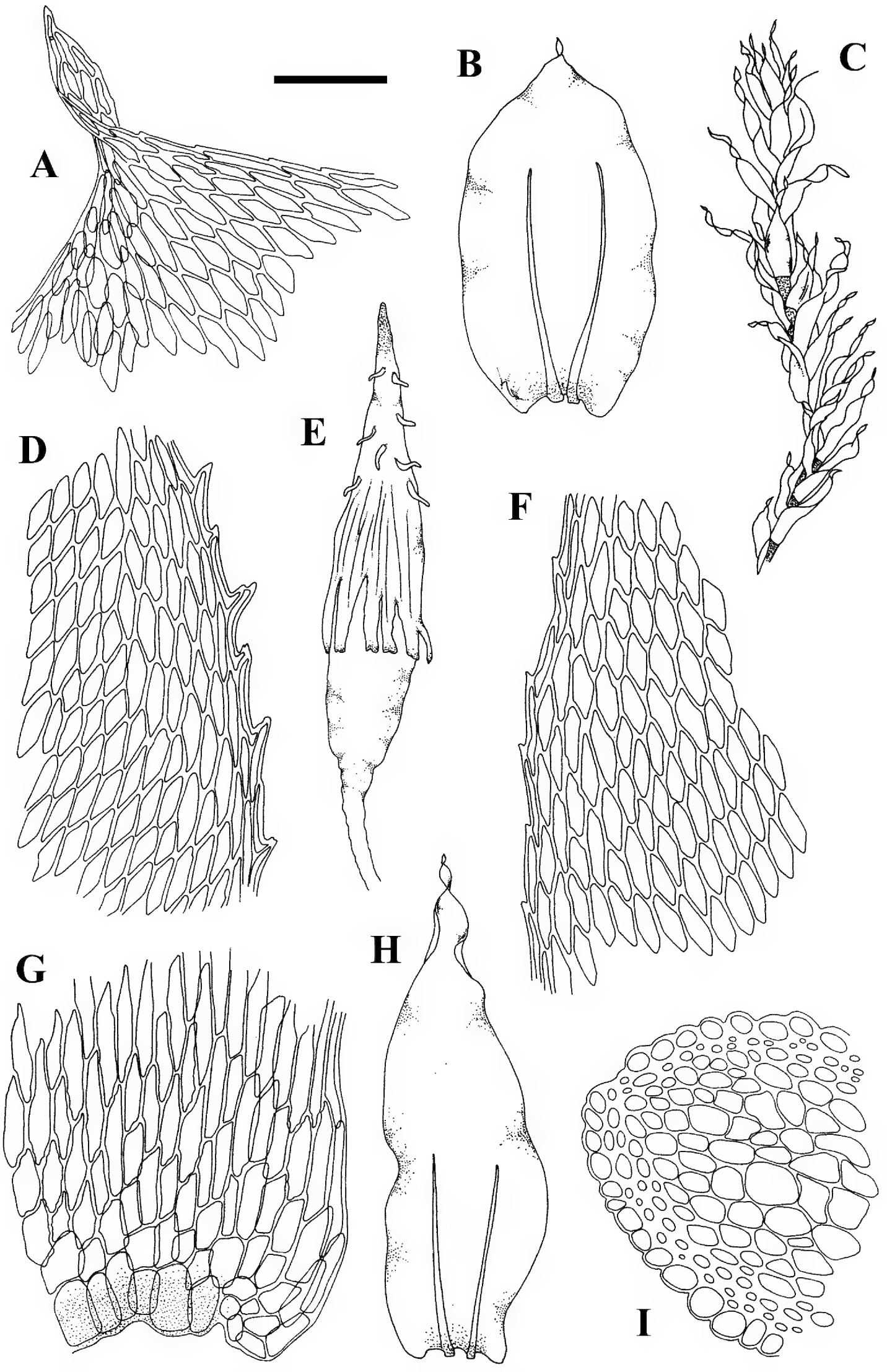


Figure 188. *Lepidopilum amplirete*. A. Leaf apex. B. Leaf, *apiculatum*-form. C. Habit. D. Upper leaf cells and margin. E. Seta, capsule, and calyptra. F. Median leaf cells and margin. G. Basal and alar cells. H. Leaf, *complanate*-form. I. Stem in cross section. Scale in mm: bar = 0.08 (I); bar = 0.09 (A, D, F, G); bar = 0.5 (B, H); bar = 0.9 (E); bar = 1.56 (C). A, F, G from *Godfrey 66213*; D from *Skutch 2530* (type *L. skutchii*); H from *Allen 8818*; all other figure parts from *Liesner 1945*.

de Waard (1986, Fig. 134); Churchill (1988, Figs. 35, 50–51); Sharp *et al.* (1994, Fig. 614); Duarte Bello (1997, Pls. 228 & 230); Buck (1998, Pl. 14 6–13); Buck (2003, Fig. 93). Figure 188.

Habitat. On twigs, lianas, palm fronds, branches, trunks, and logs; 20–1400 m.

Distribution in Central America. GUATEMALA. Quetzaltenango: *Bauer* (FH); Sacatepéquez: *Standley 58125* (F, FH). COSTA RICA. Alajuela: *Brenes 21438* (F, FH); Cartago: *Godfrey 66213* (MO, NY); Limón: *Gutiérrez 180* (F, FH); Puntarenas: *Liesner 1945* (CR, MO, NY); San José: *Skutch 3023* (FH, MO, NY, US). PANAMA. Canal Area: *Nee 9054* (MO); Chiriquí: *Cornman 3006* (F, FH, MO); Coclé: *Hunter & Allen 432B* (MO); Darién: *Allen 8944* (MO).

World range: Mexico; Central America; Caribbean; Western and Northern South America.

Lepidopilum amplirete is a medium-sized species with glossy, yellowish green plants. In Central America the species occurs most often on twigs or small branches, and as a result its secondary stems are usually erect. The leaves of *L. amplirete* are crispate to contorted when dry and sometimes distinctly flattened when wet. There is, however, considerable variation in leaf stance, and some collections have leaves that are evenly foliate when wet. Stems that are flattened when wet tend to have obovate to spathulate lateral leaves, but evenly foliate stems have all leaves oblong to oblong-ovate. There is also considerable variation in the costae and leaf marginal development among collections of *L. amplirete*. The upper margins can vary from subentire to sharply serrate, while the costae can be short (1/4 the leaf length) and slender or long (2/3 the leaf length) and project at the tips. A fairly consistent feature of *L. amplirete* is the tendency for the leaves to have twisted tips whether wet or dry. The upper leaf cells in *L. amplirete* are relatively short, rhomboidal to fusiform, and usually thick-walled. At times the leaves appear to be indistinctly bordered by a single row of elongate cells. Plants of *L. amplirete* often have asexual propagula that occur at the tips of the leaves, along the leaf margins, or abaxial to the leaf insertions at the base of the costae.

In Central America *Lepidopilum amplirete* is autoicous and nearly always has capsules. However, Churchill (1988) and Buck (1998) reported the species as dioicous, and Caribbean collections rarely have sporophytes (Buck 1998). The setae are long, fairly slender, smooth below, and papillose above. There is considerable variation in setae length, and the variation appears to have two modes: in some collections they range from 5–9 mm long, while in others they are 9–13 mm long. The ovoid- to oblong-cylindrical capsules in *L. amplirete* have exothecial cells that are more strongly collenchymatous than those of any other Central American *Lepidopilum*.

Lepidopilum cubense and *L. amplirete* were described in the same publication; Buck (1998) synonymized them and chose *L. amplirete* as the name for the combined taxon because the type of *L. cubense* was a mixed collection. Bartram (1951) took a narrower view of this species and considered it a species complex (consisting of *L. cubense*, *L. apiculatum*, and *L. skutchii*) characterized by scarcely bordered leaves with short, hexagonal-elliptic upper cells and setae that were smooth below but papillose above. According to Bartram, members of the complex varied in leaf shape, degree of marginal serrations, apex form, costal length, and setae length. Churchill (1988) took an opposite view of this species complex and synonymized *L. cubense*, *L. apiculatum*, and *L. skutchii*. At the same time, he indicated there were two distinct forms of the species that were perhaps different at the subspecies or species level. If the complex is formally recognized at the species level, the oldest names for the two forms are *L. amplirete* and *L. semilaeve*.

In Central America *L. amplirete* can be confused with *L. surinamense* or *L. longifolium*. All three species have similarly shaped, mostly elimbate leaves with fusiform upper cells. *Lepidopilum amplirete* is the only one of the three that has asexual gemmae at the tips of its leaves or on the leaf margins. Many collections of *L. amplirete* differ from *L. longifolium* in having somewhat flattened, widely spaced leaves with sharply serrate margins, but there are some collections with closely spaced, evenly foliate leaves and subentire margins. *Lepidopilum longifolium* differs from all forms of *L. amplirete* in its longer acuminate leaf apices and setae that are spinose throughout. When sporophytes are present, *L. surinamense* clearly differs from *L. amplirete* in having shorter (2.5–3.0 mm vs. 5–13 mm), stout setae and longer capsules (1.5–2.5 mm vs. 1.5–2.0 mm), but, in the absence of sporophytes, separation of the two species can be extremely difficult. *Lepidopilum surinamense* has closely spaced, evenly foliate leaves and, on this basis, it can be separated from the *L. amplirete* form with somewhat flattened, widely spaced leaves. There are, however, collections of *L. amplirete* and *L. surinamense* that are identical in aspect. *Lepidopilum surinamense* nearly always has dense masses of rhizoids on its pri-

mary stems. These rhizoids are very different from those found in most other members of *Lepidopilum*, because they are densely, at times pinnately or bipinnately, branched. Although occasionally the primary stems of *L. amplirete* are densely covered by rhizoids, the rhizoids in this species are only sparsely and irregularly branched.

3. *Lepidopilum brevipes* Mitt., J. Linn. Soc., Bot. 12: 376. 1869. Protologue. Andes Peruvianae, Tavalosos (3000 ped.), *Spruce*. Type. Tavalosos, Andes Peru, 3000 ft. *Spruce* (FH, isotype).

Lepidopilum antillarum Mitt., J. Linn. Soc., Bot. 12: 377. 1869. Protologue. Hab. Ins. S. Vincentis, *Guilding, Parker*; Barbadoes, *Parker* (Herb. Hooker).

Lepidopilum decaisnei Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 228. 1872. Protologue. [Mexico] Cordova (*Sallé* in herb. Decaisne).

Lepidopilum laetenitens Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32(3): 194. 1893. Protologue. [Costa Rica] Boruca (*Pitt.*[*ier*] *n° 5660*). Haut Hacum, près de Buenos Aires ([*Pittier*] *n° 5661).* Type. Herb. F. Renauld. Costa Rica–Boruca. leg. *Tonduz*, 1891 (NY, isotype).

Lepidopilum decaisnei Besch. var. *brevicuspis* Cardot, Rev. Bryol. 38: 41. 1911. Protologue. [Mexico] État de Vera Cruz: Xico, rochers humides (*Barnes & Land*, 1906).

Plants slender, 2–6 cm long, light to dark green, in lax tufts. Primary stems prostrate and creeping. Secondary stems erect-ascending, or pendent, sparsely branched, hyaline to yellowish when young, becoming reddish with age, complanate-foliate; stems in cross section with well-developed hyalodermis, 1–3 layers of small, thick-walled subepidermal cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong, hyaline; rhizoids on primary stems and at base of secondary stems, from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves distantly spaced, not or weakly dimorphic, flattened, erect-spreading to spreading, crispate to flexuose when dry, falcate-spreading when wet, ovate-lanceolate to lanceolate (dorsal leaves at times oblong-lanceolate), 2–3 mm long, asymmetric, short- or long-acuminate; margins serrate above, plane above, often broadly infolded on one side at base, elimbate; costae double, slender, 1/4–1/2 the leaf length, diverging throughout, smooth at back, not projecting at the apices; cells smooth, upper cells narrowly to broadly fusiform, 60–140 × 8–18 µm, thin-walled, not porose, becoming oblong-rectangular to oblong-fusiform below; alar cells not differentiated. Asexual propagula fusiform, multicellular, uniseriate, from clusters of initials abaxial to the leaf insertions at base of costae. Autoicous or synoicous. Setae short, 1.5–3.0 mm long, red to reddish orange, papillose throughout. Capsules erect, oblong-cylindrical, 0.5–1.0 mm long, neck well developed; exothecial cells reddish, oblate in 2–3 rows at mouth, those below oblong to rectangular, firm-walled, vertical walls considerably thicker than the horizontal walls, not collenchymatous; stomata rudimentary, 3–4-celled, on neck; opercula high-conic, 0.5–0.7 mm long; annuli of 10–12 rows of thin-walled cells, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome very narrowly triangular, median furrow absent, dorsal (outer) surface broad, whitish yellow, lightly papillose throughout, trabeculae thin, median lines faint, ventral (inner) surface narrow, 1/3 or less the width of the dorsal surface, red, lightly papillose, deposition thick; endostome as long as the exostome, pale yellowish, papillose throughout, basal membranes high, segments broad, concave-keeled, not perforate, cilia absent. Spores rounded, 10–14 µm, smooth to lightly papillose. Calyptrae campanulate-mitrate, 0.7–1.0 mm long, reddish yellow, irregularly lobed at base, scabrous above, naked or occasionally with a few multicellular ramenta.

Illustrations. Bartram (1949, Fig. 137 G–J); Churchill (1988, Fig. 27); Sharp *et al.* (1994, Fig. 613); Churchill (1994, Fig. 10 E–H); Churchill and Linares (1995, Fig. 41 a–g); Buck (1998, Pl. 15 9–15); Gradstein *et al.* (2001, Fig. 168 D–H); Buck (2003, Fig. 94). Figure 189.

Habitat. On trees, slender branches or shrubs, vines, twigs, palm fronds, palm or fern pinnae, and fallen logs; 300–2000 m.

Distribution in Central America. BELIZE. Cayo: *Allen 18369* (MO); Toledo: *Allen 18672* (MO). GUATEMALA. San Marcos: *Crosby 2846* (MO, NY); Suchitepéquez: *Standley 66914* (F, FH). HONDURAS. Comayagua: *Allen 11066* (MO, TEFH); Lempira: *Allen 11410* (MO); Yoro: *Allen 13559*

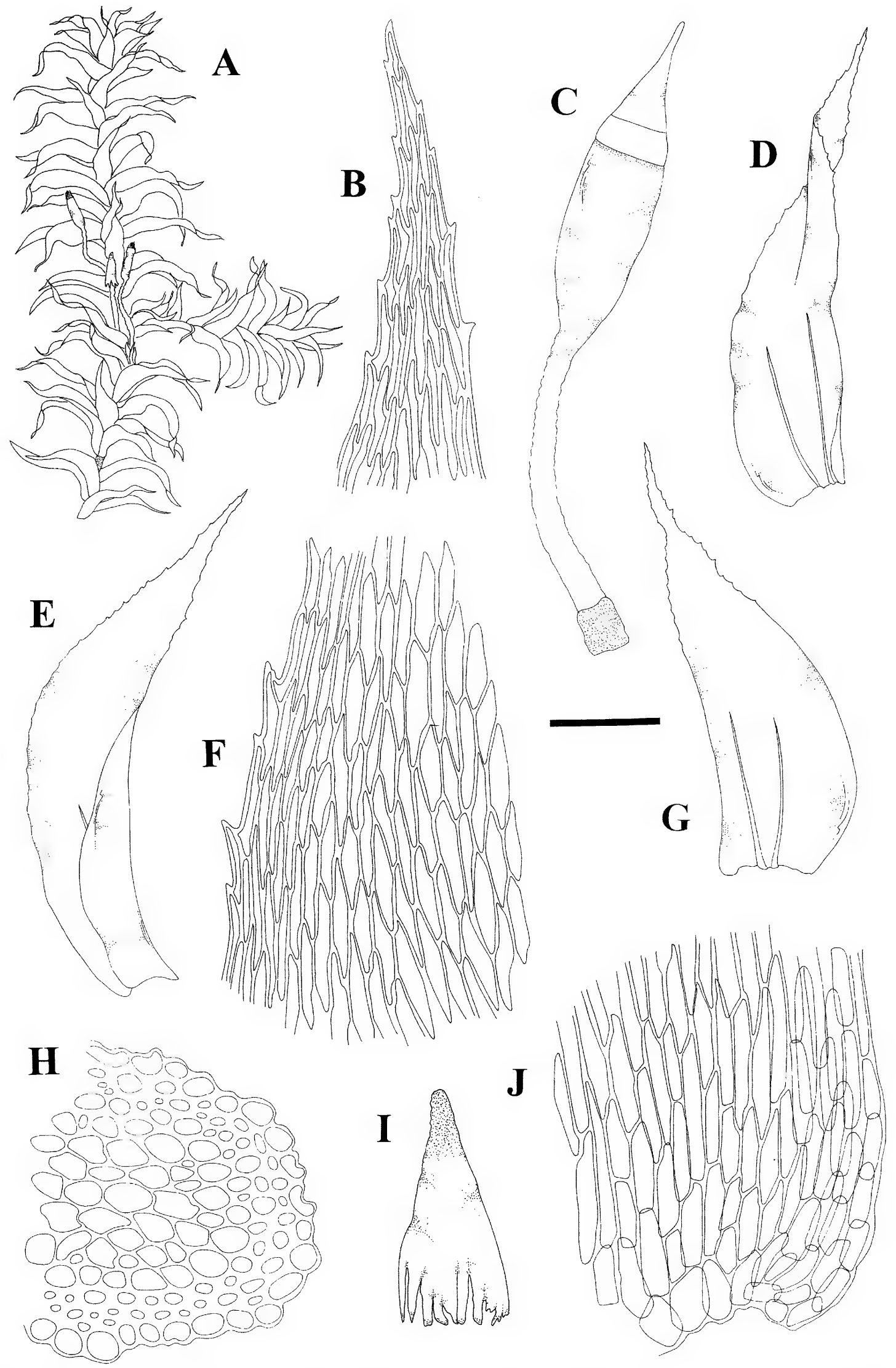
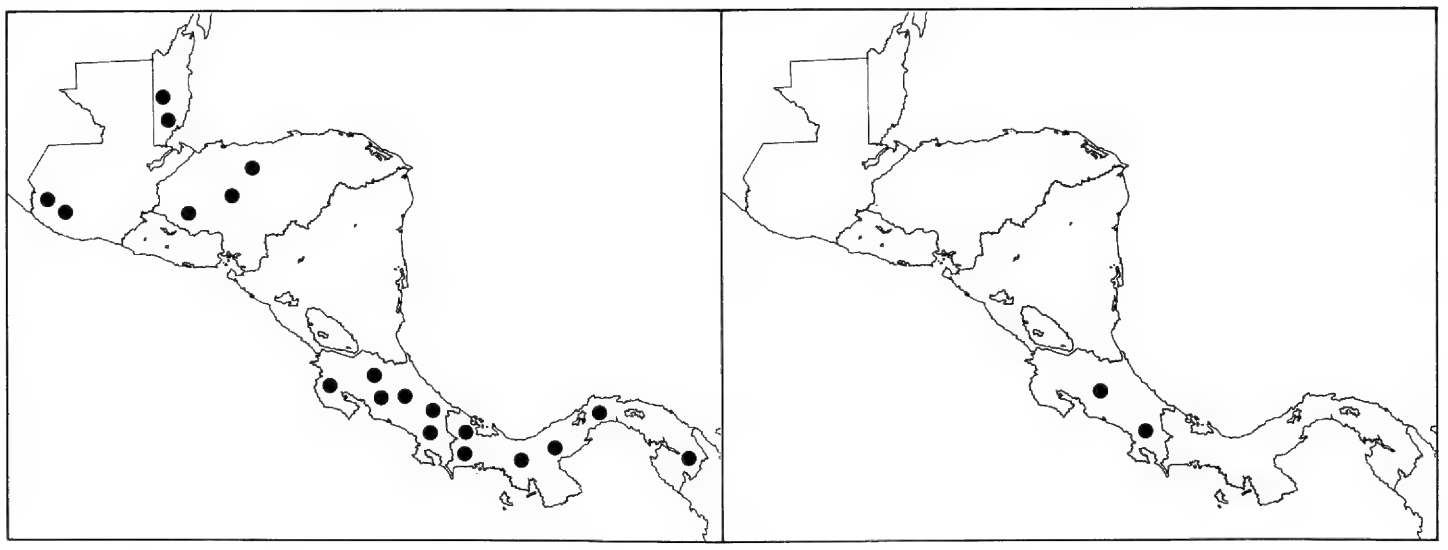


Figure 189. *Lepidopilum brevipes*. A. Habit. B. Leaf apex. C. Seta, capsule, annulus, and operculum. D, E & G. Leaves. F. Median leaf cells and margin. H. Stem in cross section. I. Calyptra. J. Basal and alar cells. Scale in mm: bar = 0.08 (H); bar = 0.09 (B, F, J); bar = 0.7 (I); bar = 0.9 (C–E, G); bar = 2.6 (A). C, I from *Whittemore 5673*; all other figure parts from *Allen 18369*.



Lepidopilum brevipes *Lepidopilum curvifolium*

(MO, TEFH). COSTA RICA. Alajuela: *Brenes 19012b* (FH); Cartago: *Crosby & Crosby 5791* (MO); Guanacaste: *Traña 58* (MO); Limón: *Gutiérrez 212a* (F, FH, NY); Puntarenas: *Crosby 13140* (MO); San José: *Crosby & Crosby 5877* (MO). PANAMA. Bocas del Toro: *Allen 5103* (MO); Chiriquí: *Salazar 4890* (MO); Coclé: *McPherson 7658B-6* (MO); Darién: *Williams 1057* (F, NY); Panamá: *Seemann* (NY); Veraguas: *Nee 9886* (MO).

World range: Mexico; Central America; Caribbean; Northern and Western South America, Brazil.

Lepidopilum brevipes is a small species that in Central America most often grows on twigs or vines. It has distantly spaced, slender, ovate-lanceolate to lanceolate leaves that are complanate and usually falcate. When dry the plants typically have erect-spreading, somewhat crispate to flexuose leaves. Its leaves are not or weakly dimorphic and typically asymmetric, although the dorsal leaves are sometimes oblong-lanceolate and more or less symmetric; they are short- to long-acuminate. The leaves in *L. brevipes* have thin-walled, narrowly to broadly fusiform upper cells; costae that end at or just below midleaf; and unbordered margins that are serrate above. In Central America *L. brevipes* is synoicous or autoicous; most collections have abundant sporophytes that have short setae and are papillose throughout. The calyptrae are typically naked, but occasionally they may have a few multicellular ramenta.

The slender plants of *Lepidopilum brevipes*, as well as the narrow, distantly spaced, falcate, ovate-lanceolate to lanceolate leaves, give the species a distinct aspect that helps in recognizing it under a hand lens. In Central America *L. brevipes* can be confused with those *Lepidopilum* species that have elimbate, falcate leaves: *L. muelleri*, *L. scabrisetum*, and *L. cuspidans*. All three species differ from *L. brevipes* in having calyptrae that are usually densely beset with multicellular ramenta. Although forms of *L. brevipes* with long-acuminate leaves are especially similar to *L. muelleri*, that species is larger in size (leaves 3–5 mm long) and has longer setae (5–13 mm long) than *L. brevipes*. *Lepidopilum scabrisetum* has short-acuminate leaves and is easily confused with expressions of *L. brevipes* with that form of leaves. Most collections of *L. scabrisetum* are more robust than *L. brevipes* and they usually have broader leaves, but there are forms of *L. scabrisetum* that are gametophytically identical to *L. brevipes*. *Lepidopilum scabrisetum* often has deciduous leaves, and this is very helpful in distinguishing it from *L. brevipes*. However, the features that best distinguish *L. scabrisetum* from *L. brevipes* are the above noted calyptral differences and setae length (4–10 mm vs. 1–3.5 mm). *Lepidopilum cuspidans* is similar in size to *L. brevipes* and both species have short setae. It differs from *L. brevipes* only in having erect rather than erect-spreading leaves, spinose rather than papillose setae, and in calyptral ornamentation.

The protologue for *Lepidopilum laetenitens* implies Pittier collected the type, but the isotype at NY was collected by Tonduz. However, the number associated with *L. laetenitens* in the protologue is an exsiccatae number rather than a collection number. Tonduz, an assistant to Pittier, made many of the collections issued by Pittier and Durand in their *Plantae Costaricenses Exsiccatae* (Sayre 1975).

4. *Lepidopilum curvifolium* Mitt., J. Linn. Soc., Bot. 12: 374. 1869. Protologue. [Ecuador] Andes Quitenses, fl. Bombonasa (1200–2000 ped.), *Spruce, n. 724*. Types. Bombonasa, *Spruce 724* (NY, holotype; NY (2), isotypes).

Lepidopilum gertrudis Herzog, Biblioth. Bot. 87: 137. 1916. Protologue. [Bolivia] An Baum- und Gesträuchästen im Bergwald des Rio Tocorani, ca. 2200 m, [*Herzog*] *No. 4020*.

Lepidopilum rotundifolium E. B. Bartram, Bryologist 54: 239. 1951 [1952]. Protologue. [Costa Rica] General, elev. 800 m, *A. Alfaro 160*, Aug. 22, 1934. Type. Plants of Costa Rica. General, el. 800 m, Aug. 22, 1934. *No. 160. Anastasio Alfaro*, Collector (FH, holotype), *syn. nov.*

Plants medium-sized to robust, 4–8 cm long, light to dark green, greenish yellow, in lax tufts. Primary stems prostrate and creeping. Secondary stems erect or ascending, not or sparsely branched, hyaline to yellowish when young, becoming red to red brown with age, slightly complanate-foliate or evenly foliate; stems in cross section with small hyalodermis, 3–5 layers of small, thick-walled subepidermal cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong, hyaline; rhizoids usually on primary stems and at base of secondary stems, from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves distant, somewhat flattened, weakly dimorphic, erect, flexuose-contorted when dry, erect-spreading when wet. Lateral leaves broadly ovate to ovate-oblong, 4–5 mm long, symmetric or weakly asymmetric, short-acuminate, apex often twisted and pinched; margins entire below, serrate to serrulate above, limbate, border weak, of 2–3 rows of elongate cells, plane above, broadly infolded on one side at base; costae double, stout, ending at or near midleaf, diverging throughout, smooth at back, not projecting at the apex; cells smooth, median cells rhomboidal to hexagonal, 50–84 × 22–30 µm, firm-walled, often porose, lower cells elongate-rhomboidal to rectangular, porose; alar cells not differentiated. Dorsal leaves erect when wet, broadly ovate to oval, 3–5 mm long, symmetric, short-acuminate; margins entire below, serrate to serrulate above, limbate, border weak, of 2–3 rows of elongate cells, plane. Asexual propagula fusiform, multicellular, uniseriate, arising from clusters of initials abaxial to the leaf insertions at base of costae. Dioicous. Intact sporophytes not seen from Central America, description from *Spruce 783*, NY (Ecuador), *Cerón 34835-A*, MO (Ecuador), *Smith C314A*, MO (Peru), and *Frahm et al. 344*, MO (Peru). Setae short, 3–8 mm long, red to reddish orange, smooth at base, densely spiculose-papillose above. Capsules erect, ovoid to oblong-cylindrical, 1.5–2.0 mm long, neck well developed; exothecial cells reddish, oblate in 2–3 rows at mouth, those below oblong to rectangular, firm-walled, not collenchymatous; stomata rudimentary, 3–6-celled, on neck; opercula high-conic, 1.0 mm long; annuli of 6–9 rows of thin-walled cells, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome very narrowly triangular, median furrow absent, dorsal (outer) surface broad, whitish yellow, lightly papillose throughout, trabeculae thin, median lines faint, ventral (inner) surface narrow, 1/3 or less the width of the dorsal surface, dark red, lightly papillose, deposition thick; endostome as long as the exostome, pale yellowish, papillose throughout, basal membranes high, segments broad, concave-keeled, not perforate, cilia absent. Spores rounded, 12–16 µm, smooth to lightly papillose. Calyptrae campanulate-mitrate, 1.7–2.0 mm long, reddish yellow, irregularly lobed at base, scabrous, with many multicellular ramenta.

Illustrations. Herzog (1916, Fig. 60); Welch (1974, Figs. 385–393, as *L. rotundifolium*); Churchill (1988, Fig. 47); Churchill (1994, Fig. 11 D & E). Figure 190.

Habitat. On forest trees.

Distribution in Central America. COSTA RICA. Puntarenas: *Crosby 2613* (MO); San José: *Alfaro 160* (FH).

World range: Mexico; Central America; Western South America.

Lepidopilum curvifolium is a robust species with well-developed, erect to ascending secondary stems. When dry the plants typically have large, rigid, erect to weakly complanate leaves that are somewhat contorted-twisted. Its leaves are weakly dimorphic, with somewhat asymmetric, broadly ovate to ovate-oblong lateral leaves and symmetric, broadly ovate dorsal leaves. All leaves are short-

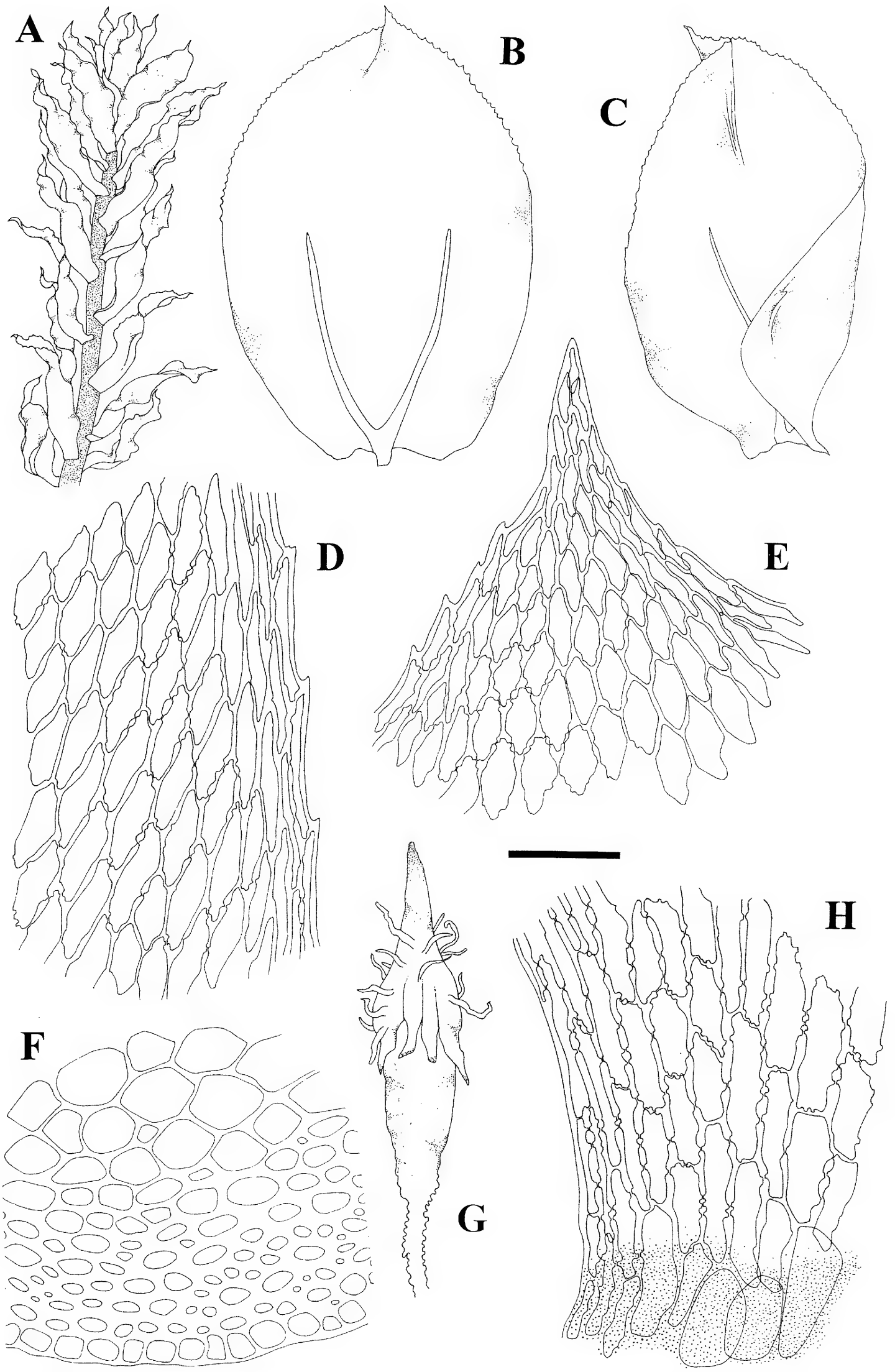


Figure 190. *Lepidopilum curvifolium*. A. Habit. B & C. Leaves. D. Median leaf cells and margin. E. Leaf apex. F. Stem in cross section. G. Seta, capsule, and calyptra. H. Basal and alar cells. Scale in mm: bar = 0.08 (F); bar = 0.09 (D, E, H); bar = 0.9 (B, C, G); bar = 2.5 (A). G from *Frahm 344*; all other figure parts from *Crosby 2613*.

acuminate, often twisted or pinched at the apex, and they have firm-walled, often porose cells that are hexagonal to rhomboidal above and elongate-hexagonal below. Its costae end at or just above mid-leaf, and although remarkably stout for the genus, they are smooth at back and do not project at the tips. The leaf margins are serrate to serrulate above and weakly bordered by 2–3 rows of narrow, elongate cells. *Lepidopilum curvifolium* is dioicous and mature sporophytes are unknown in Central America. South American collections of *L. curvifolium* have short setae that are spiculose-papillose above, but smooth at the base.

In size *L. curvifolium* approaches *L. polytrichoides*, but that species has very long (5.5–8.0 mm), usually broadly ovate-lanceolate, long-acuminate lateral leaves. Both species have short setae, but *L. polytrichoides* is synoicous and often has sporophytes. In both wet and dry aspects, cellular areolation, and sexual condition (dioicous) *L. curvifolium* is similar to *L. surinamense* and *L. permarginatum*. *Lepidopilum surinamense* also resembles *L. curvifolium* in having weakly bordered leaves and short setae, but it has shorter (2.5–3.2 mm long) lateral leaves. Florschütz-de Waard (1986) and Churchill (1988) considered *L. rotundifolium* a robust expression of *L. surinamense*, but that taxon is here treated as a synonym of *L. curvifolium*. *Lepidopilum permarginatum* differs from *L. curvifolium* in its longer setae (11–14 mm long) and leaves that are strongly bordered by 6–15 rows of cells. The Mexican *Lepidopilum apophysatum* Hampe *ex* Besch. is very similar to *L. curvifolium* in size, as well as leaf shape and areolation. It differs from *L. curvifolium* primarily in having more or less complanate-foliate stems, with leaves that are smooth when dry. Typically, the stems of *L. curvifolium* are evenly foliate with flexuose-contorted leaves when dry. The two taxa may be synonymous; *L. curvifolium* is the older name.

5. *Lepidopilum cuspidans* Mitt., J. Linn. Soc., Bot. 12: 378. 1869. Protologue. [Ecuador] Andes Quitenses, in sylva Canelos (3000 ped.), *Spruce, n. 757.*

Plants slender, to 6 cm long, yellowish green, in lax tufts. Primary stems prostrate and creeping. Secondary stems erect-ascending, or pendent, not or sparsely branched, hyaline to yellowish when young, becoming reddish with age, complanate-foliate; stems in cross section with hyalodermis, 1–3 layers of small, thick-walled subepidermal cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong, hyaline; rhizoids on primary stems and at base of secondary stems, from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves distantly spaced, not or weakly dimorphic, flattened, erect to erect-spreading, crispate to flexuose when dry, erect-spreading when wet, ovate-lanceolate to lanceolate (dorsal leaves at times oblong-lanceolate), 2–3 mm long, asymmetric, long-acuminate; margins serrate above, plane above, often broadly infolded on one side at base, elimbate to obscurely limbate; costae double, slender, 1/2 the leaf length, diverging throughout, smooth at back, not projecting at the apex; cells smooth, upper cells narrowly to broadly fusiform, 50–120 × 8–18 µm, thin-walled, not porose, becoming oblong-rectangular to oblong-fusiform below; alar cells not differentiated. Asexual propagula not seen. Autoicous. Setae short, 1.5–3.0 mm long, red to reddish orange, densely scabrose to spinose throughout. Capsules erect, oblong-cylindrical, 1.0 mm long, neck well developed; exothecial cells reddish, oblate in 2–3 rows at mouth, those below oblong to rectangular, firm-walled, vertical walls considerably thicker than the horizontal walls, not collenchymatous; stomata rudimentary, 3–4-celled, on neck; opercula high-conic, 0.5–0.8 mm long; annuli of 10–12 rows of thin-walled cells, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome very narrowly triangular, median furrow absent, dorsal (outer) surface broad, whitish yellow, lightly papillose throughout, trabeculae thin, median lines faint, ventral (inner) surface narrow, 1/3 the width of the dorsal surface, red, lightly papillose, deposition thick; endostome as long as the exostome, hyaline to pale yellow, papillose throughout, basal membranes high, segments broad, concave-keeled, not perforate, cilia absent. Spores rounded, 10–12 µm, smooth to lightly papillose. Calyptrae campanulate-mitrate, 1.7–1.3 mm long, reddish yellow, irregularly lobed at base, scabrous above, calyptrae with many multicellular ramenta.

Illustration. Figure 191.
Habitat. In tropical wet forest; 450–500 m.

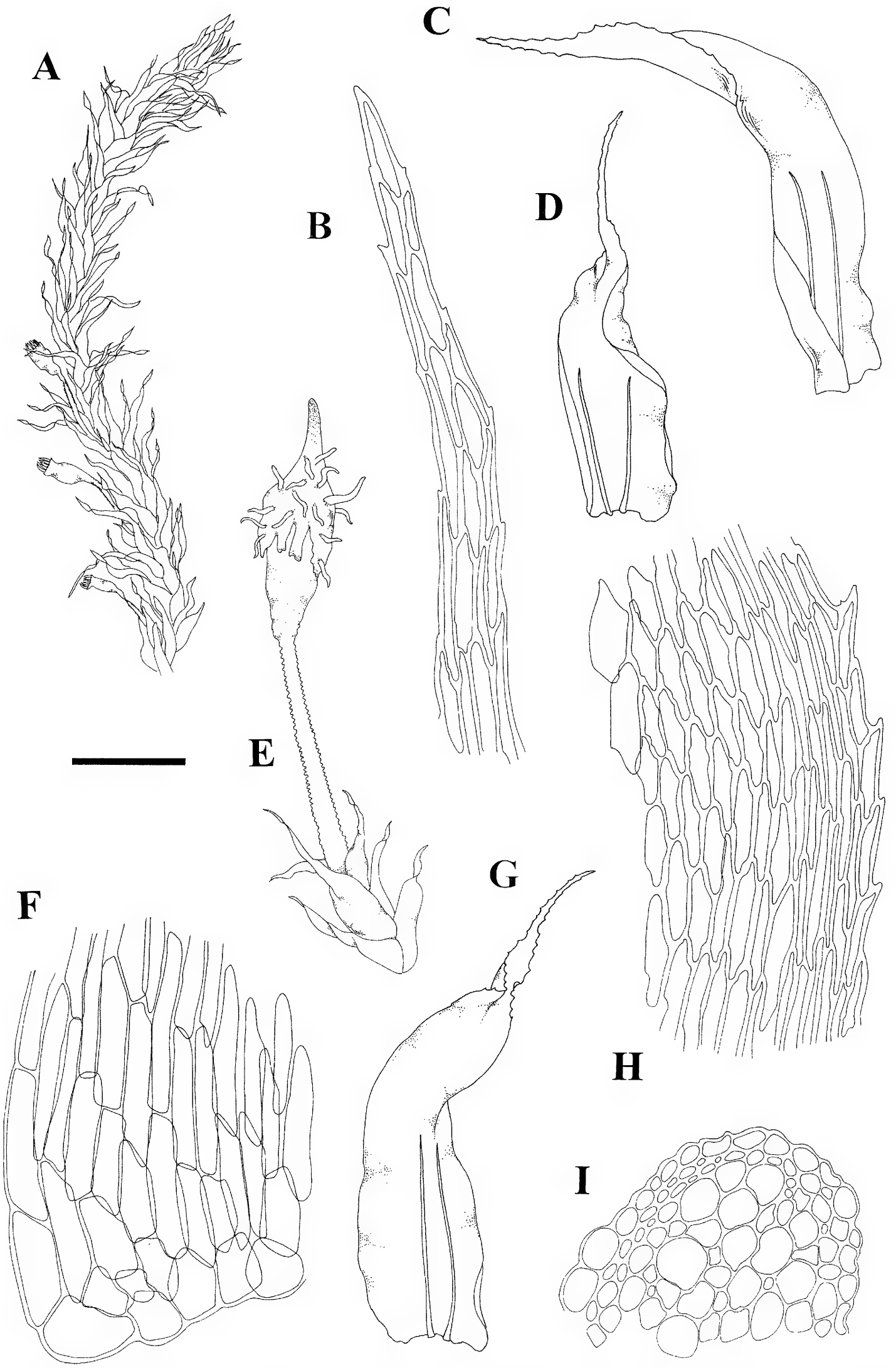
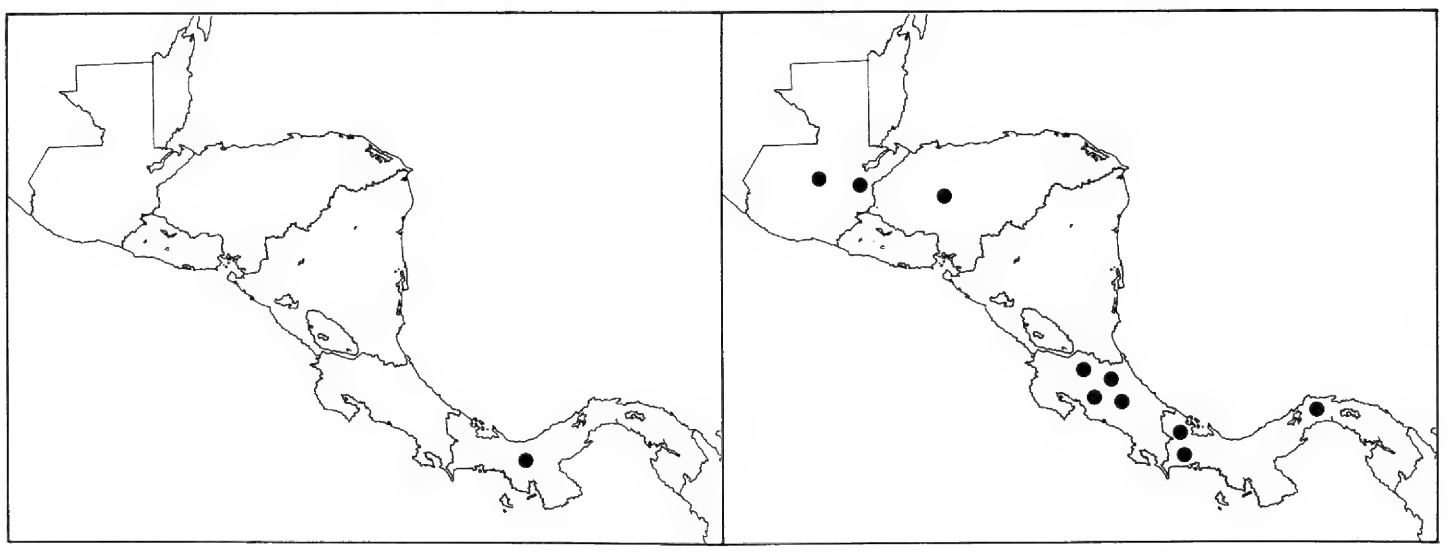


Figure 191. *Lepidopilum cuspidans*. A. Habit. B. Leaf apex. C & G. Lateral leaves. D. Dorsal leaf. E. Seta, capsule, and calyptra. F. Basal and alar cells. H. Median leaf cells and margin. I. Stem in cross section. Scale in mm: bar = 0.09 (B, F, H); bar = 0.13 (I); bar = 0.7 (C, D, G); bar = 0.9 (E); bar = 2.6 (A). All figure parts from *Nee & Mori 14304A*.



Lepidopilum cuspidans *Lepidopilum diaphanum*

Distribution in Central America. PANAMA. Veraguas: *Nee & Mori 14304A* (MO).
World range: Central America; Western South America.

Lepidopilum cuspidans is a slender species known in Central America from a single Panamanian collection. It has asymmetric, ovate-lanceolate to lanceolate leaves that are distantly spaced and more or less complanate. The leaves are erect to erect-spreading, crispate to flexuose when wet or dry, and long-acuminate. The leaves of *L. cuspidans* have thin-walled, narrowly to broadly fusiform upper cells, and costae that end at or a little above midleaf. Although some leaves appear to be obscurely bordered above, most leaves are elimbate. Churchill (1988) described *L. cuspidans* as dioicous, but the single Central American collection is autoicous. Its sporophytes have short, scabrose or spinose setae. The calyptrae are densely beset with multicellular ramenta.

Lepidopilum brevipes is very similar to *L. cuspidans* in its slender size, narrow, distantly spaced, falcate, ovate-lanceolate to lanceolate leaves, and short setae. Although some plants of *L. brevipes* have short-acuminate leaves, the species is variable in this respect and other collections have long-acuminate leaves. The leaves of *L. brevipes* differ somewhat from those of *L. cuspidans* in being more wide-spreading and not as strongly crispate-flexuose, but the best features that distinguish *L. brevipes* from *L. cuspidans* are found in their calyptrae and setae ornamentation. *Lepidopilum brevipes* has papillose setae and calyptrae that are naked or have only a few multicellular ramenta.

6. *Lepidopilum diaphanum* (Hedw.) Mitt., J. Linn. Soc., Bot. 12: 382. 1869. *Hypnum diaphanum* Hedw., Sp. Musc. Frond. 243. 1801. *Pterygophyllum diaphanum* (Hedw.) Brid., Muscol. Recent. Suppl. 4: 150. 1819. *Hookeria diaphana* (Sw. ex Hedw.) Hook. & Grev., Edinburgh J. Sci. 2: 227. 1825. Protologue. Jamaica, locis udis; secundum hepaticam aliquam plantulam; jungermaniae *pingui* similem, quae basi mei exempli adhaerebat [*Swartz*]. Types. Fl. Ind. Occid., *Swartz* (FH, NY, isotypes).

Lepidopilum huallagense Broth., Hedwigia 45: 282. 1906. Protologue. Peru: Rio Huallaga, Cerro de Escalero, 1100 m, an Wasserfällen ([*Ule*] *n. 2382, 2383*). Type. E. Ule Herbarium Brasiliense Amazonas-Expedition. An Wasserfällen des Cerro de Escalero, 1100 m. Peru, Departamento Loreto, März 1903, *No. 2383* (FH, syntype).

Lepidopilum vesicularioides E. B. Bartram, Fieldiana, Bot. 25: 314. 1949, invalid name, lacks a description. Based on: Guatemala. Dept. Zacapa: along Rio del Volcán de Monos, Volcán de Monos, alt. 1150–2100 m, *Julian A. Steyermark 42374*, Jan. 10, 1942 (F, FH, NY).

Cyclodictyon brittoniae E. B. Bartram, Contr. U.S. Natl. Herb. 26: 100. 1928. Protologue. La Hondura, Province of San José, Costa Rica, altitude 1300 to 1700 meters, *Paul C. Standley and Juvenal Valerio*, March 9, 1926, *no, 51882a*. Types. Plants of Costa Rica. La Hondura, Province of San José, alt. 1300–1700 meters, Mch. 9–1926, *Paul C. Standley & Juvenal Valerio 51882a* (NY, US, isotypes), *syn. nov.*

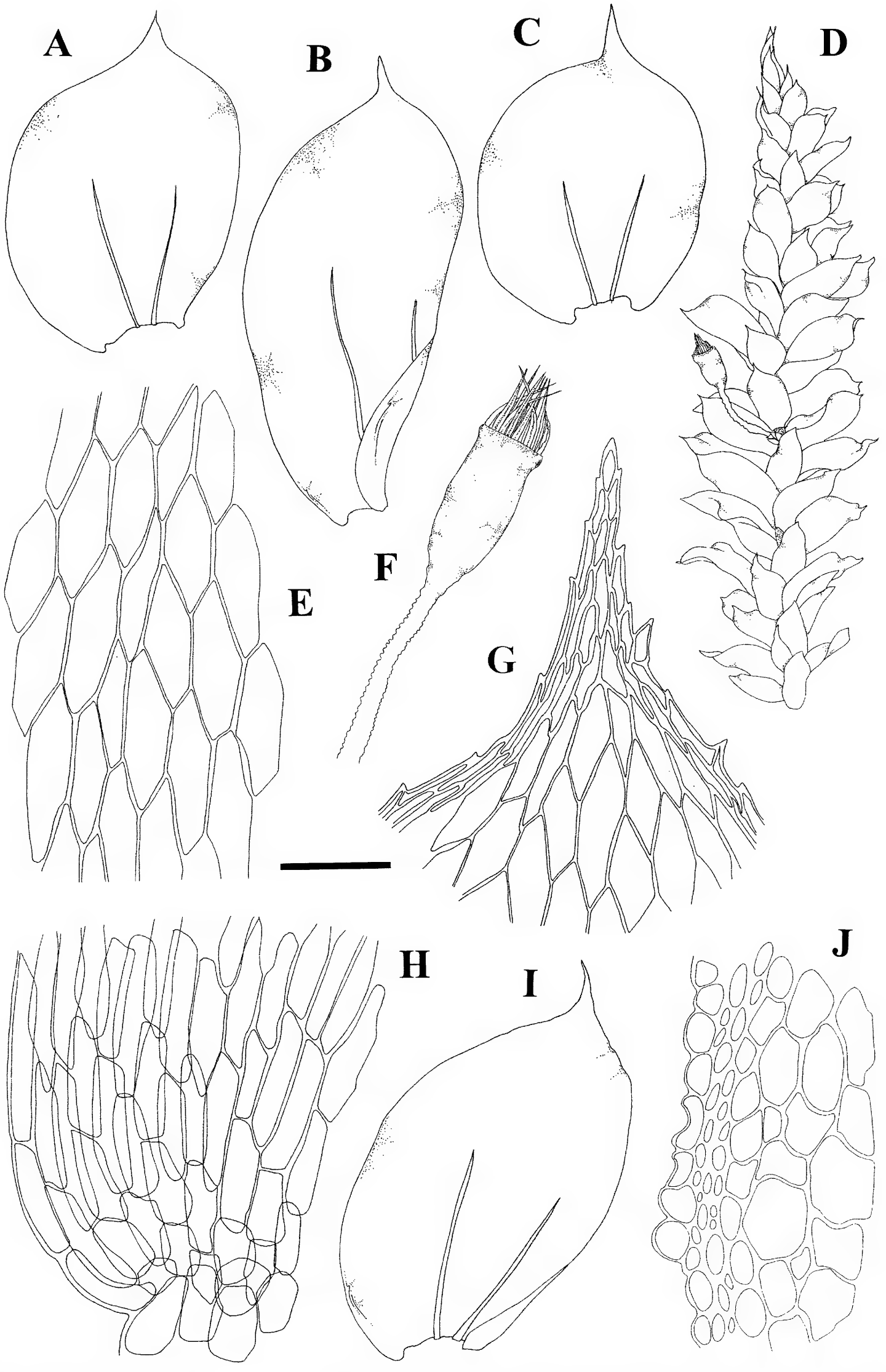


Figure 192. *Lepidopilum diaphanum*. A & C. Dorsal leaves. B & I. Lateral leaves. D. Habit. E. Median leaf cells. F. Seta and capsule. G. Leaf apex. H. Basal and alar cells. J. Stem in cross section. Scale in mm: bar = 0.08 (J); bar = 0.09 (E, G, H); bar = 0.7 (A–C, I); bar = 0.9 (F); bar = 2.5 (D). All figure parts from *Crosby 5904*.

Plants medium-sized, 2–7 cm long, pale, glaucous green, greenish yellow, or reddish, in lax tufts. Primary stems prostrate and creeping. Secondary stems prostrate, erect, ascending, or pendent, at times attenuate, not or sparsely branched, hyaline to yellowish when young, becoming red to red brown with age, complanate-foliate; stems in cross section with well-developed hyalodermis, 1–2 layers of small, thick-walled subepidermal cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong, hyaline; rhizoids on primary stems and on secondary stems when in contact with substrate, from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves crowded to somewhat distant, variously dimorphic, somewhat flexuose to flattened when dry, flaccid when wet. Lateral leaves erect- to wide-spreading, obovate, ovate-oblong, ovate-lanceolate, occasionally lanceolate in epiphyllous forms, 2.0–3.5 mm long, weakly to strongly asymmetric, short- to long-acuminate; margins serrulate to serrate to spinose above, entire below, limbate, border weak or well developed by 2–4 rows of elongate cells, plane above, broadly infolded on one side at base; costae double, thin, ending 1/3–2/3 the leaf length, diverging throughout, smooth at back, not projecting at the apex; cells smooth, median cells hexagonal, rhomboidal, or broadly fusiform, 120–160 × 30–50 µm, lax-walled, lower cells rectangular; alar cells not differentiated. Dorsal leaves erect to appressed when wet, ovate, oblong-ovate, or suborbicular, 2 mm long, symmetric, short- to long-acuminate; margins entire, serrulate to serrate to spinose above, limbate, border weak or well developed by 2–4 rows of elongate cells, plane. Asexual propagula usually present, especially abundant on attenuate branch tips, propagula fusiform, multicellular, uniseriate, arising from clusters of initials abaxial to the leaf insertions at base of costae. Dioicous. Setae short, 1–2 mm long, red to reddish orange, densely papillose throughout. Capsules erect, ovoid to oblong-cylindrical, 1.0–1.2 mm long, neck weakly developed; exothecial cells reddish, oblate in 2–3 rows at mouth, those below oblong to rectangular, evenly firm- to thick-walled, not collenchymatous; stomata rudimentary, 3–6-celled, on neck; opercula high-conic, 0.7–1.0 mm long; annuli of 7–9 rows of thin-walled cells, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome very narrowly triangular, median furrow absent, dorsal (outer) surface broad, whitish yellow, lightly papillose throughout, trabeculae thin, median lines faint, ventral (inner) surface narrow, 1/3 or less the width of the dorsal surface, dark red, lightly papillose, deposition thick; endostome as long as the exostome, pale yellowish, densely papillose throughout, basal membranes high, segments broad, concave-keeled, not perforate, cilia absent. Spores rounded, 12–16 µm, smooth to lightly papillose. Calyptrae campanulate-mitrate, 1 mm long, reddish yellow, irregularly lobed at base, scabrous, usually with few to many multicellular ramenta.

Illustrations. Hedwig (1801, Pl. 61 1–6); Bartram (1928a, Fig. 30 G–J, as *Cyclodictyon brittoniae*); Bartram (1949, Fig. 139 G–I); Welch (1971b, Figs. 193–198); Churchill (1988, Fig. 46); Buck (1998, Pl. 14 1–5). Figure 192.

Habitat. On twigs, leaves, and slender stems, less often on logs, rotting wood, tree trunks, herbaceous stems, pendent from trees, roots, humus or soil, and rocks or ledges; 800–2100 m.

Distribution in Central America. GUATEMALA. Baja Verapaz: *Sharp 2700* (FH, US); Zacapa: *Steyermark 42374* (F, FH, NY). HONDURAS. Comayagua: *Allen 13705* (MO). COSTA RICA. Alajuela: *Bowers 730*-a (MO); Cartago: *Griffin et al. 209* (F, MO, NY); Heredia: *Crosby & Crosby 5785* (BM, CR, F, FH, H, MO, NY, US); San José: *Crosby & Crosby 5869* (CR, MO, NY). PANAMA. Bocas del Toro: *Allen 5812* (MO, PMA); Chiriquí: *Allen 5445* (MO); Panamá: *Crosby 10088* (MO, PMA).

World range: Central America; Caribbean; Western and Northern South America.

Lepidopilum diaphanum is medium-sized species with stems that are strongly complanate-foliate and flattened whether wet or dry. It has well-developed, creeping primary stems and secondary stems that can be prostrate, erect, or pendent. Although the species grows on a very broad range of substrates, typically the plants are found on small stems, twigs, or leaves. Its leaves are extremely variable in shape, and some of the variation, especially the narrow epiphyllous forms, appears to be correlated with the substrate type on which the plants grow. The leaves are variously dimorphic with asymmetric, obovate to broadly ovate-lanceolate lateral leaves and symmetric broadly ovate to suborbicular

dorsal leaves; both can be short- or long-acuminate. The upper leaf cells in *L. diaphanum* are extremely large and lax, and they vary from hexagonal to rhomboidal, or broadly fusiform. The basal cells are variously rectangular and the alar cells are undifferentiated. The leaves have thin costae that end above midleaf, are smooth at back, and do not project at the tips, while the entire, serrulate, or serrate upper margins are bordered by 1–3 rows of narrow, elongate cells. *Lepidopilum diaphanum* is dioicous; its setae are very short and densely papillose throughout. Plants often have clusters of multicellular, uniseriate propagula found on the abaxial side of the leaf insertions. At times the secondary stems are attenuate. The attenuate tips are usually densely beset with propagula and appear to represent specialized asexual structures.

Lepidopilum diaphanum is the most distinctive species of *Lepidopilum* in Central America. Its very flattened-complanate plants look more like *Hookeria acutifolia* than *Lepidopilum*, and its remarkably enlarged, lax upper leaf cells are similar to those of *Hookeria* or *Cyclodictyon.* Indeed, the leaf cells in *L. diaphanum* are so distinctive that the species can often be recognized with a dissecting microscope. In Central America *L. polytrichoides* and *L. tortifolium* also have large leaf cells that approach in size those of *L. diaphanum. Lepidopilum polytrichoides*, however, is a much larger plant than *L. diaphanum*, with sharply serrate to spinose lateral leaves that are typically over 5 mm long. *Lepidopilum tortifolium* differs from *L. diaphanum* in having more strongly bordered leaves that are crispate-contorted when dry. Plants of *Lepidopilum scabrisetum* can be as strongly complanate-flattened as those of *L. diaphanum*; however, *L. scabrisetum* has elimbate leaves, narrow (10–15 μm) leaf cells, and long (5–10 mm) setae. *Hookeria acutifolia* differs from *L. diaphanum* in having ecostate leaves and exostome teeth that are densely cross-striate on the dorsal (outer) surface. Plants of *Cyclodictyon* differ from *L. diaphanum* in having less dimorphic leaves with generally isodiametric upper leaf cells, and exostome teeth that are densely cross-striate on the dorsal surface.

7. *Lepidopilum exiguum* B. H. Allen, *sp. nov.* Type. Panama. Veraguas: stream valley 10.4 km along road leading NW from Escuela Agricola "Alto de Piedra," 5.4 km NW of Santa Fe, 08°30′N, 081°05′W, *Marshall R. Crosby 10161* (MO, holotype).

Species haec a *L. inflexo* statura gracili et foliis leniter limbatis differt.

Plants slender, 4–5 cm long, light to dark green, in lax tufts. Primary stems prostrate and creeping. Secondary stems erect-ascending, or pendent, sparsely branched, hyaline to yellowish when young, becoming reddish with age, evenly foliate; stems in cross section with hyalodermis, 1–3 layers of small, thick-walled subepidermal cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong, hyaline; rhizoids usually on primary stems and at base of secondary stems, from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves distantly spaced, not dimorphic, erect, flexuose-contorted when dry, erect-spreading, somewhat complanate when wet, leaves ovate-oblong to obovate, 1.8–2.2 mm long, symmetric or weakly asymmetric, abruptly short-acuminate; margins plane above, often broadly infolded on one side at base, limbate, by 2–4 rows of elongate cells; costae double, slender, 2/3 the leaf length, diverging throughout, smooth at back, not projecting at the apices; cells smooth, upper cells rhomboidal to hexagonal, 40–60 × 18–22 μm, firm-walled, often porose, becoming broadly fusiform to elongate-rhomboidal or rectangular below, sometimes porose; alar cells not differentiated. Asexual propagula not seen. Dioicous. Setae short, 2–3 mm long, red to reddish orange, papillose throughout. Capsules erect, oblong-cylindrical, 0.5–1.0 mm long, neck well developed; exothecial cells reddish, oblate in 2–3 rows at mouth, those below oblong to rectangular, firm-walled, not collenchymatous; stomata rudimentary, 3–6-celled, on neck; opercula high-conic, 0.5 mm long; annuli of 5–8 rows of thin-walled cells, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome very narrowly triangular, median furrow absent, dorsal (outer) surface broad, whitish yellow, lightly papillose throughout, trabeculae thin, median lines faint, ventral (inner) surface narrow, 1/3 or less the width of the dorsal surface, dark red, lightly papillose, deposition thick; endostome as long as the exostome, pale yellowish, papillose throughout, basal membranes high, segments broad, concave-keeled, not perforate, cilia absent. Spores

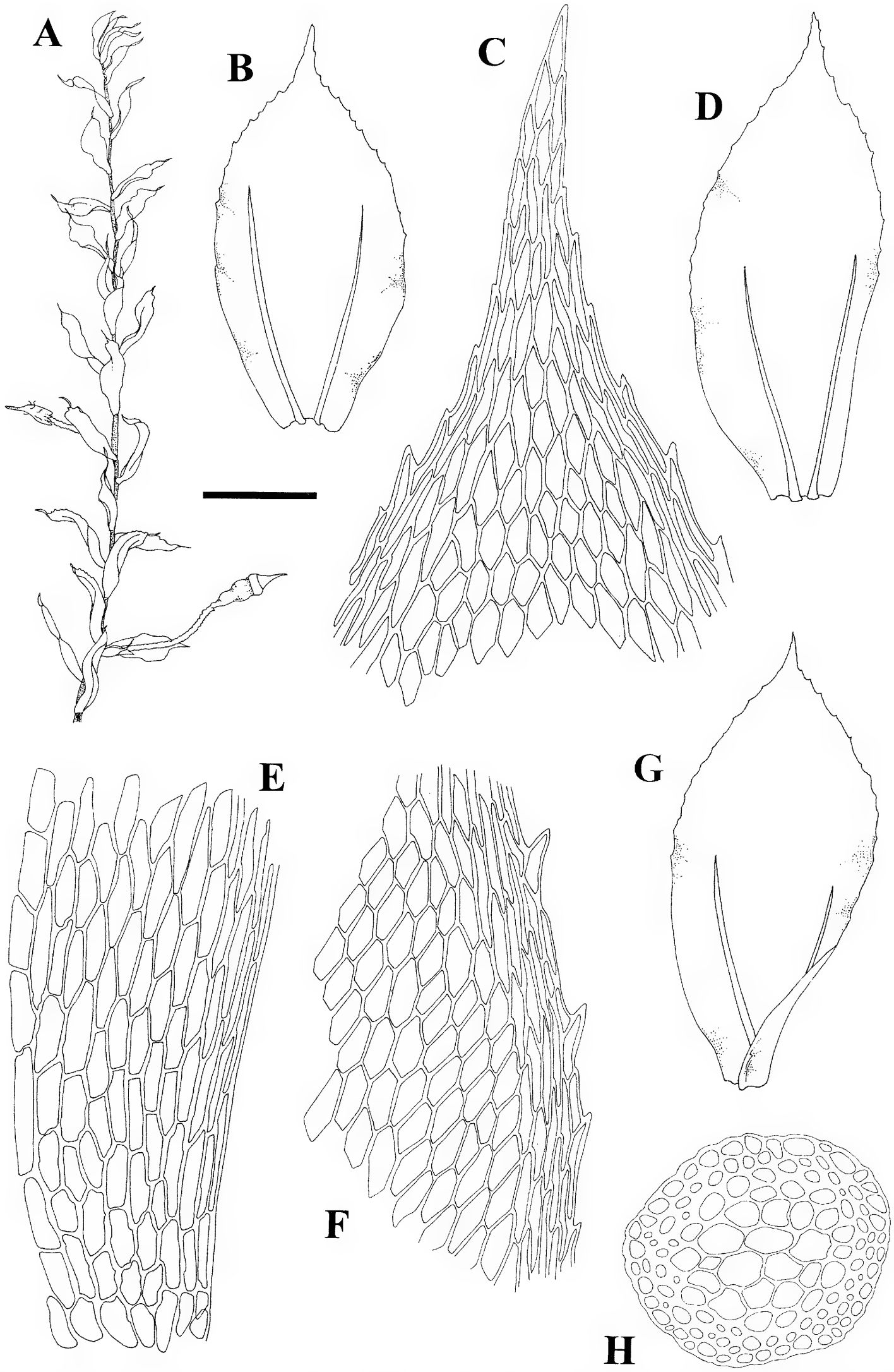
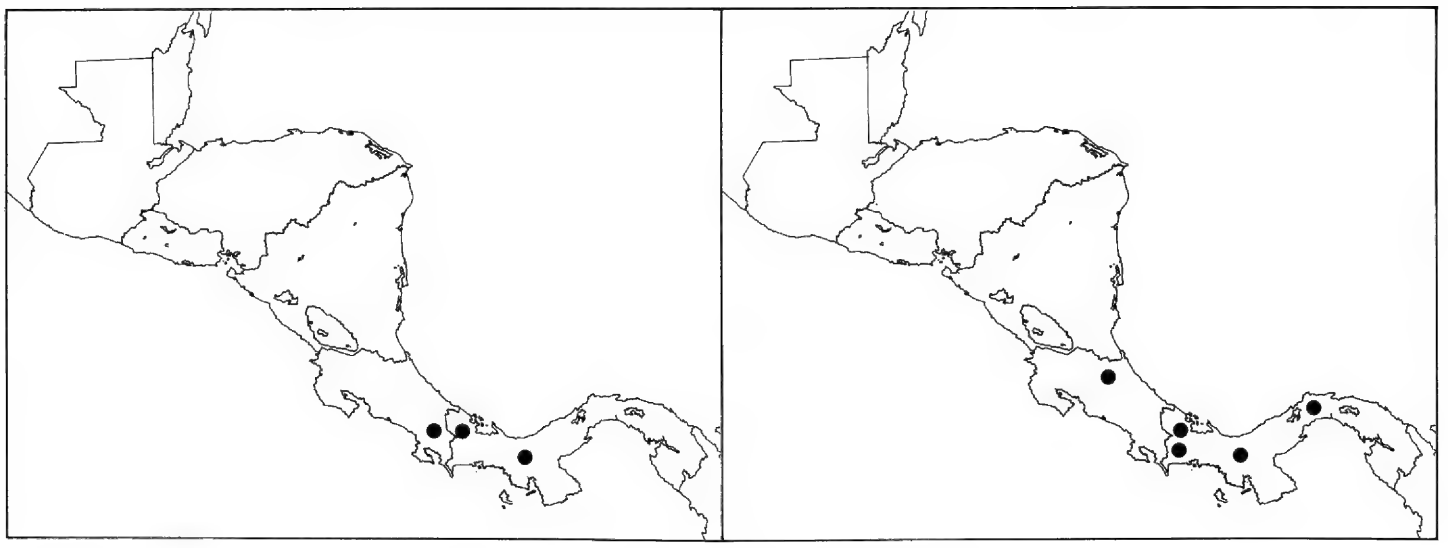


Figure 193. *Lepidopilum exiguum*. A. Habit. B. Dorsal leaf. C. Leaf apex. D & G. Lateral leaves. E. Basal and alar cells. F. Median leaf cells and margin. H. Stem in cross section. Scale in mm: bar = 0.08 (H); bar = 0.09 (C, E, F); bar = 0.5 (B, D, G); bar = 1.96 (A). All figure parts from *Crosby 10161* (type).



Lepidopilum exiguum *Lepidopilum inflexum*

rounded, 12–14 µm, smooth to lightly papillose. Calyptrae campanulate-mitrate, 1 mm long, reddish yellow, irregularly lobed at base, scabrous above, naked or with a few multicellular ramenta.

Illustration. Figure 193.

Habitat. On tree trunks and pendent from slender stems; 350–1200 m.

Distribution in Central America. COSTA RICA. Puntarenas: *Dauphin 2011* (MO). PANAMA. Bocas del Toro: *Hammel 13691B* (MO); Veraguas: *Crosby 10161* (MO).

World range: Central America.

Lepidopilum exiguum is a slender species with distantly spaced, ovate-oblong to obovate leaves. When dry the plants typically have erect, somewhat contorted-twisted leaves that are evenly foliate, but when wet the plants have erect to erect-spreading somewhat complanate leaves. Its leaves are not dimorphic; they are usually weakly asymmetric, due to the broad infolding on one lower leaf margin, and abruptly short-acuminate. The leaves have firm-walled, hexagonal to rhomboidal upper cells; costae that end above midleaf; and serrate to serrulate upper margins bordered by 2–4 rows of narrow, elongate cells. The sporophytes have short, papillose setae; the calyptrae are naked or have only a few multicellular ramenta.

The very slender plants of *Lepidopilum exiguum* along with its distantly spaced, ovate-oblong to obovate leaves separate it from all other Central American species of *Lepidopilum* with distinctly bordered leaves except *L. ultramarginatum*. That species, however, has very strongly bordered leaves (7–14 rows of elongate cells at base) and long (10–12 mm), spinose setae. Also, in *L. ultramarginatum* one fork of the costae is usually merged along most of its length with the leaf border. *Lepidopilum exiguum* is also similar to *L. brevipes* because both are slender species with well-spaced leaves and short setae. *Lepidopilum brevipes* differs from *L. exiguum* in having strongly asymmetric, elimbate leaves and narrowly fusiform upper leaf cells.

8. *Lepidopilum inflexum* Mitt., J. Linn. Soc., Bot. 12: 375. 1869. Protologue. [Ecuador] Andes Quitenses, in sylva Canelos (2000 ped.), *Spruce, n. 726*; ibidem forma gracilior, *Spruce, n. 727*; in monte Abitagua (4000 ped.), forma robustior, *Spruce, n. 728*. Types. Mont. de Canelos, *Spruce 726* (NY, lectotype, designated here); Mont. de Canelos, *Spruce 727* (NY, syntype); Mont. Abitagua, *Spruce 728* (NY, syntype); In mont. Abitagua, *Spruce 728* (NY, syntype).

Plants medium-sized, 3–7 cm long, dark green, yellowish red, or reddish, in lax tufts. Primary stems prostrate and creeping. Secondary stems erect or ascending, not or sparsely branched, hyaline to yellowish when young, becoming reddish with age; stems in cross section with hyalodermis, 1–3 layers of small, thick-walled subepidermal cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, red-

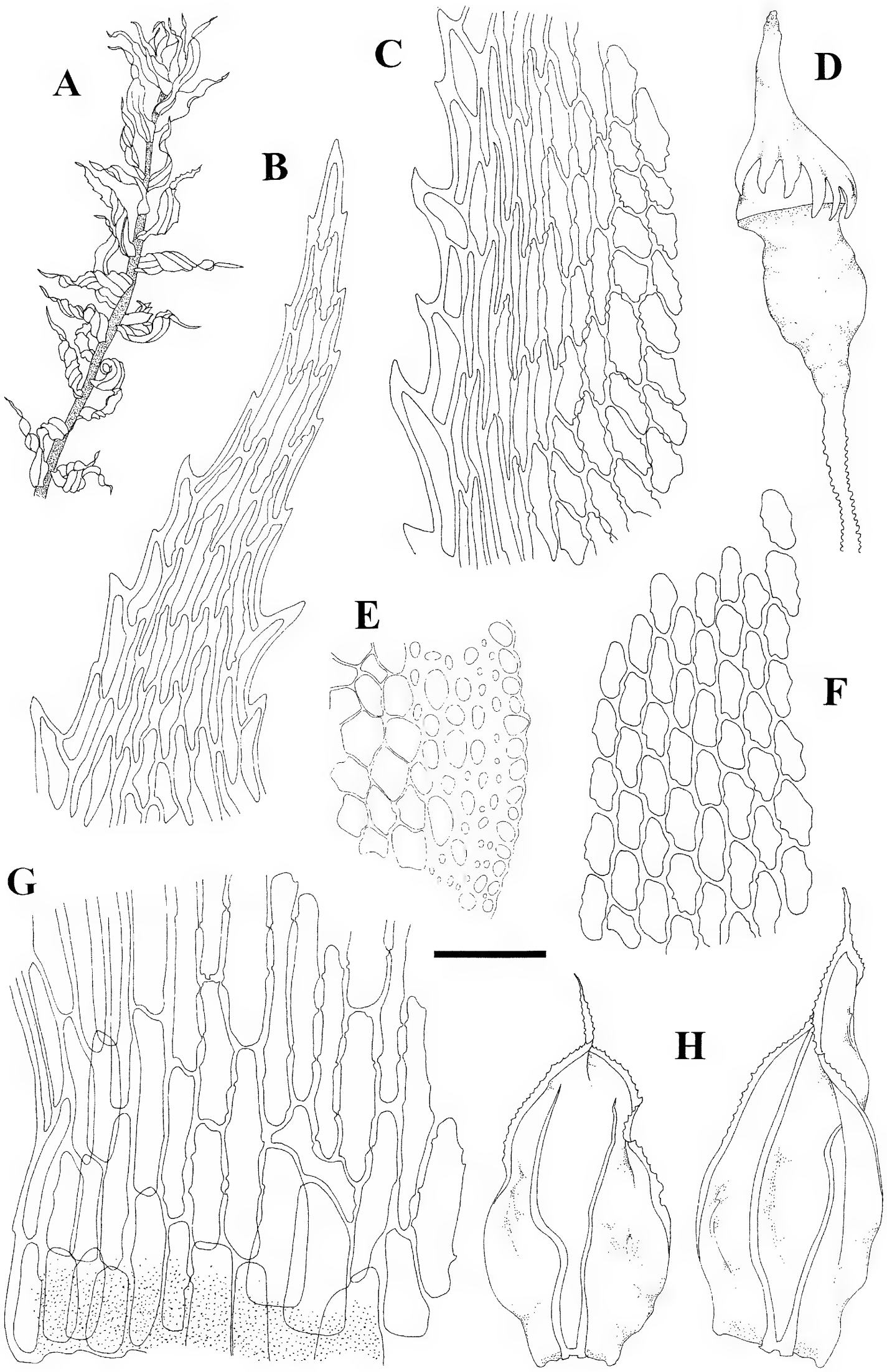


Figure 194. *Lepidopilum inflexum*. A. Habit. B. Leaf apex. C. Median leaf cells and margin. D. Seta, capsule, and calyptra. E. Stem in cross section. F. Median leaf cells. G. Basal and alar cells. H. Leaves. Scale in mm: bar = 0.06 (B, C, F, G); bar = 0.08 (E); bar = 0.6 (D); bar = 0.9 (H); bar = 1.96 (A). B, F, G from *Allen 5436*; all other figure parts from *Crosby 10221*.

dish brown, upper cell oblong, hyaline; rhizoids usually on primary stems and at base of secondary stems, from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves distantly spaced, regularly distributed, not dimorphic, erect, tortuose-contorted when dry, flexuose-contorted when wet, ovate-oblong, 2.5–3.5 mm long, symmetric, concave, abruptly short-or long-acuminate; margins sharply serrate above, plane, limbate, by 2–4 rows of elongate cells; costae double, strong, 2/3–3/4 the leaf length, diverging throughout, smooth at back, often projecting at the apices; cells smooth, upper cells rhomboidal to hexagonal, 30–60 × 18–22 µm, firm-walled, usually porose, becoming broadly fusiform to elongate-rhomboidal, long-rectangular at base, porose; alar cells not differentiated. Asexual propagula not seen. Autoicous. Setae short, 3–5 mm long, red to reddish orange, papillose or spinose throughout. Capsules erect, ovoid to ovoid-oblong, 0.7–1.0 mm long, neck well developed; exothecial cells reddish, oblate in 2–3 rows at mouth, those below suboblong to rectangular, firm-walled, not collenchymatous; stomata rudimentary, 3–6-celled, on neck; opercula high-conic, 0.7–1.0 mm long; annuli of 5–8 rows of thin-walled cells, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome very narrowly triangular, median furrow absent, dorsal (outer) surface broad, whitish yellow, lightly papillose throughout, trabeculae thin, median lines faint, ventral (inner) surface narrow, 1/3 or less the width of the dorsal surface, yellow, lightly papillose, deposition thick; endostome as long as the exostome, pale yellowish, papillose throughout, basal membranes high, segments broad, concave-keeled, not perforate, cilia absent. Spores rounded, 12–14 µm, smooth to lightly papillose. Calyptrae campanulate-mitrate, 1.0–1.5 mm long, reddish yellow, irregularly lobed at base, scabrous above, naked.

Illustrations. Churchill (1988, Fig. 43). Figure 194.

Habitat. On tree bases, twigs, roots, rotting logs, and humus in forest; 350–1400 m.

Distribution in Central America. COSTA RICA. Heredia: *Grayum & Chacón 8514* (MO). PANAMA. Bocas del Toro: *Allen 5682* (MO); Chiriquí: *Allen 5436* (MO); Panamá: *Gentry & Dwyer 5599* (MO); Veraguas: *Crosby 10221* (MO).

World range: Central America; Western South America.

Lepidopilum inflexum is a medium-sized species, with evenly foliate plants and distantly spaced, ovate-oblong leaves that are strongly tortuose-twisted when dry and flexuose-twisted when wet. The symmetric leaves are not dimorphic; they are abruptly short-or long-acuminate; and they have firm-walled, hexagonal to rhomboidal upper leaf cells. The leaves have strongly developed costae ending 2/3–3/4 the leaf length that often project as single-celled spines at the tips, and sharply serrate leaf margins that are distinctly bordered above by 2–4 rows of narrow, elongate cells. Central American material of *L. inflexum* is autoicous and sporophytes are often present. They have short, papillose or spinose setae and short, ovoid to ovoid-oblong capsules. The calyptrae are naked.

In most of its features *Lepidopilum inflexum* resembles a diminutive form of *L. permarginatum.* That species, however, differs from *L. inflexum* in having larger leaves (4–5 mm long) that are sometimes doubly serrate; stronger upper leaf limbidia (4–8 rows of elongate cells); and costae that do not project at the tips. In addition, *L. permarginatum* has longer (11–14 mm) setae.

9. *Lepidopilum longifolium* Hampe, Ann. Sci. Nat., Bot. sér. 5, 4: 365. 1865. Protologue. [Colombia] Bogotá, Pacho, 2200 m, et Tequendama Escaleros 2500 m, pauca specima cum aliis intermixta leg. *A. Lindig*.

Lepidopilum robustum Mitt., J. Linn. Soc., Bot. 12: 386. 1869. Protologue. [Colombia] Andes Bogotenses, in sylvis supra Pacho (7000 ped.), *Weir, n. 134*. [Ecuador] Andes Quitenses, Tunguaragua, *Spruce*.

Lepidopilum integerrimum Mitt., J. Linn. Soc., Bot. 12: 382. 1869. Protologue. [Ecuador] Andes Quitenses, in monte Chimborazo in sylvis Cinchonae (3000–5000 ped.), *Spruce, n. 752*; in monte Tunguragua (7000 ped.), *Spruce, n. 753*; ad rivulum Lligua (7000 ped.), *Spruce, n. 754*; in monte Tunguragua, secus rivulum Vascun (Baccun) (7000 ped.), *Spruce, n. 755*.

Lepidopilum aureofulvum Müll. Hal., Linnaea 42: 495. 1879. Protologue. Venezuela. [*Fendler*] *Nr. 122b*.

Lepidopilum cladorrhizans Besch., J. Bot. (Morot) 8: 63. 1894. Protologue. Guadeloupe, rampant sur les troncs d'arbres, au morne Goyavier (*Ed. Marie, n^{o} 43*) RR.

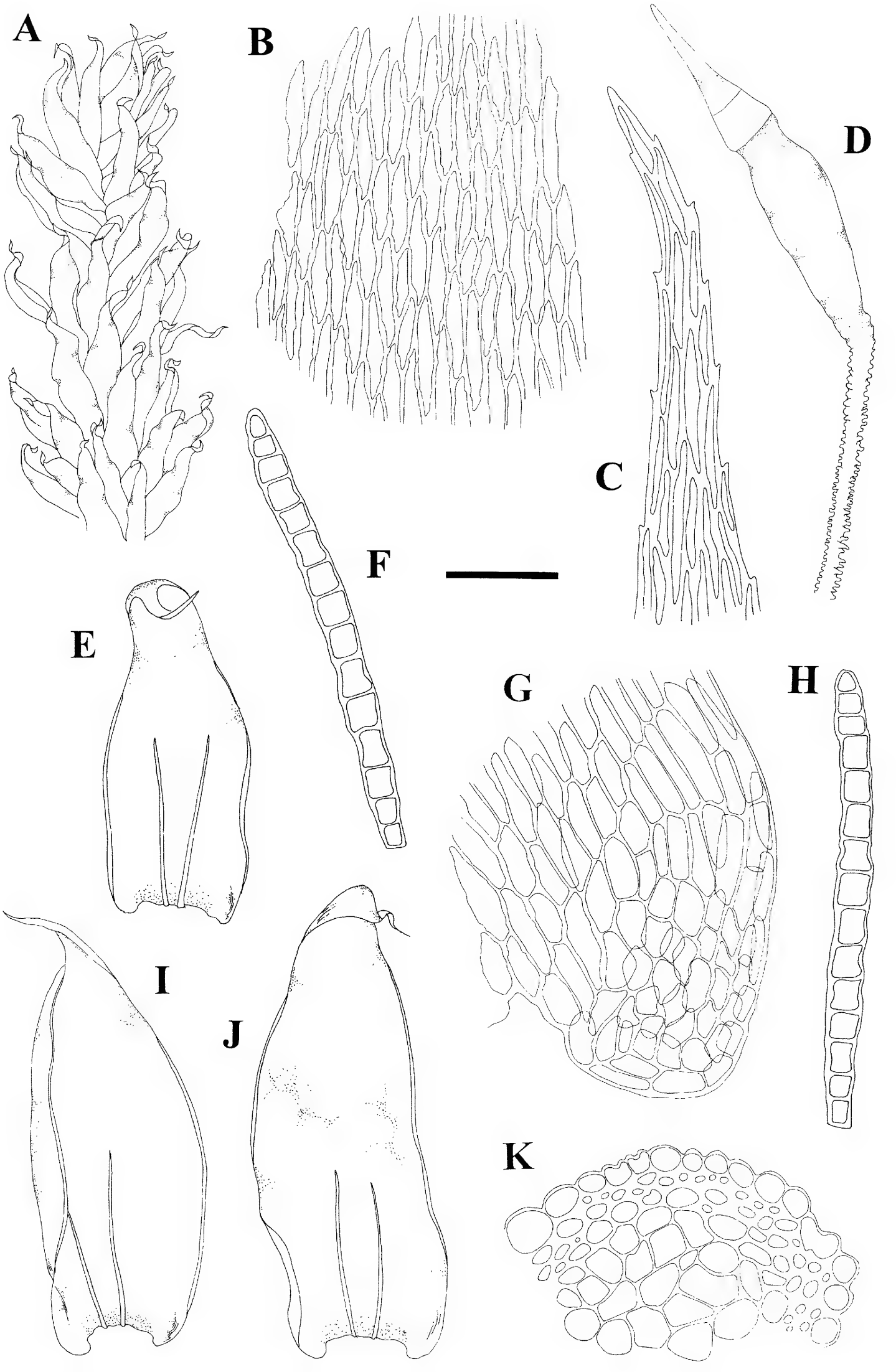
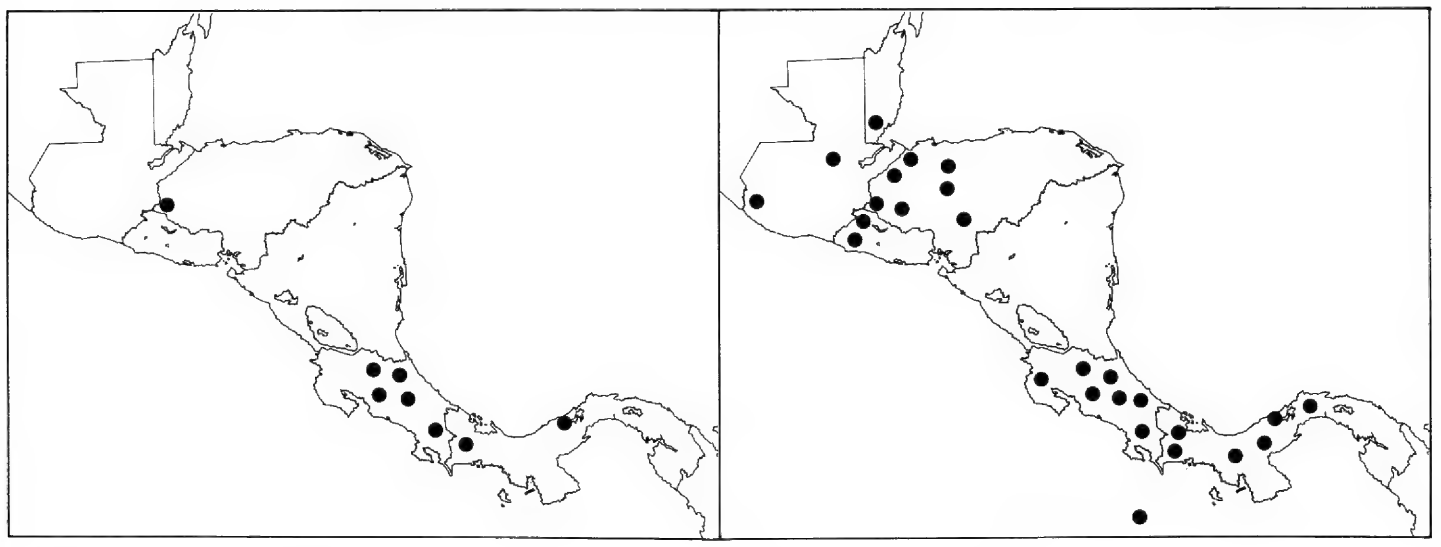


Figure 195. *Lepidopilum longifolium*. A. Habit. B. Median leaf cells. C. Leaf apex. D. Seta, capsule, annulus, and operculum. E, I & J. Leaves. F & H. Gemmae. G. Basal and alar cells. K. Stem in cross section. Scale in mm: bar = 0.06 (C, K); bar = 0.08 (B, G); bar = 0.1 (F, H); bar = 0.7 (E, I, J); bar = 0.9 (D); bar = 1.96 (A). D from *Crosby & Crosby 6025*; all other figure parts from *Crosby & Crosby 5956*.



Lepidopilum longifolium *Lepidopilum muelleri*

Lepidopilum herzogii Broth. *in* Herzog, Biblioth. Bot. 87: 135. 1916. Protologue. [Bolivia] Tocorani, alt. 2700 m, [*Herzog*] *No. 4097*.

Stenodictyon bisodalense B. H. Allen, Crosby & Magill, Lindbergia 11: 155. 1986. Protologue. Costa Rica. Dos Amigos area, near 73 km marker on Inter American Highway, SE of El Empalme. *Sphagnum-Blechnum* bog, 2680 m, 9°37′N, 83°50′W *Crosby & Crosby 5956*. Type. Costa Rica. Cartago: Dos Amigos area, near 73 km marker on Inter American Highway, SE of El Empalme. *Sphagnum-Blechnum* bog. 2680 m altitude. 9°37′N, 83°50′W, 26.iii.1973, *Marshall R. & Carol A. Crosby 5956* (MO, holotype).

Plants medium-sized to robust, 1–4 cm long, light, glossy, yellowish red, golden, or green, in tufts or mats. Primary stems prostrate and creeping. Secondary stems prostrate or ascending, not or sparsely branched, hyaline to yellowish when young, becoming red to red brown with age; stems in cross section with well-developed hyalodermis, 3–5 layers of small, thick-walled subepidermal cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong, hyaline; rhizoids on primary stems and secondary stems, from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, irregularly or densely pinnately branched. Leaves closely spaced, uniform, dense, obscuring the stem, erect or spreading when wet, erect-patent, undulate to flexuose or smooth when dry, oval-oblong, oblong, or oblong-lanceolate, 2–4 mm long, symmetric, occasionally weakly asymmetric, gradually short- or long-acuminate, apices often reflexed-recurved; margins entire, serrulate or serrate, usually narrowly recurved, at times throughout, sometimes mostly plane, elimbate; costae double, weak, 1/4–1/3 the leaf length, diverging throughout, smooth at back, not projecting at the apices; cells smooth, median cells long-fusiform to linear-fusiform, 55–185 × 10–17 µm, thick-walled, smooth or porose, lower cells rounded-rhomboidal to rectangular, thin-walled, not porose, cells across the base enlarged, subrectangular, orange red, alar region at times subauriculate, with short-rectangular cells. Asexual propagula brownish red or hyaline, fusiform, uniseriate, 13–20 cells long, arising from clusters of initials abaxial to the leaf insertions at base of costae, at times densely clustered on filiform-attenuate branch and stem tips. Autoicous. Setae elongate, 8–14 mm long, red to reddish orange, densely spinose. Capsules erect to suberect, ovoid to oblong-cylindrical, 1–2 mm long, neck well developed, lightly tuberculate; exothecial cells reddish, oblate in 4–6 rows at mouth, those below rounded, oblong, or short- to long-rectangular, thick-walled, not collenchymatous; stomata rudimentary, 3–4-celled, on neck; opercula high-conic, 1.0 mm long; annuli of 8–10 rows of thin-walled cells, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome very narrowly triangular, median furrow absent, dorsal (outer) surface broad, whitish, densely papillose throughout, trabeculae thin, median lines faint, ventral (inner) surface narrow, 1/3 the width of the dorsal surface, dark red, lightly papillose, deposition thick; endostome as long as the exostome, pale yellowish, papillose throughout, basal membranes high, segments broad, concave-keeled, not perforate, cilia absent. Spores rounded, 16–22 µm, lightly

papillose. Calyptrae campanulate-mitrate, 1.5–2.5 mm long, reddish yellow, irregularly lobed at base, with many multicellular ramenta.

Illustrations. Welch (1969, Figs. 190–198, as *L. robustum*); Allen *et al.* (1986, Figs. 1–9); Churchill (1988, Figs. 32 & 33); Duarte Bello (1997, Pl. 229, as *L. aureofulvum*; Pl. 232, as *L. robustum*); Buck (1998, Pl. 13 8–15); Vaz and Costa (2006b, Figs. 36–43). Figure 195.

Habitat. On trunks, branches, twigs, and leaves of trees or shrubs, and on rotting logs; 426–3130 m.

Distribution in Central America. HONDURAS. Ocotepeque: *Allen 14488D* (MO). COSTA RICA. Alajuela: *Crosby 3790* (MO); Cartago: *Crosby & Crosby 5794* (MO); Heredia: *Crosby & Crosby 8551* (MO); Puntarenas: *Crosby 9947* (MO); San José: *Crosby & Crosby 6118* (MO). PANAMA. Chiriquí: *Salazar 4876* (MO); Colón: *Crosby 10451* (MO).

World range: Mexico; Central America; Caribbean; Western and Northern South America.

Lepidopilum longifolium is a medium-sized to robust species with glossy, yellowish red or green plants that are typically densely and evenly foliate. Its erect leaves often have distinctly reflexed-recurved apices. Central American collections usually have symmetric, oblong-oval or oblong leaves that are flexuose-undulate when dry, but in the Caribbean (Churchill 1988) collections often have narrower, slightly asymmetric leaves. The leaf cells in *L. longifolium* are firm-walled, linear-fusiform to long-fusiform, and mostly very broad (10–17 μm). In many collections the leaves are subauriculate at base with relatively well-developed (for *Lepidopilum*) alar cells. Its costae are short, faint, and rarely reach above midleaf. The leaf margins are elimbate, but otherwise they are remarkably variable. At times the margins are narrowly recurved nearly throughout and entire, while at other times they are mostly plane and sharply serrate above. There are also many plants that exhibit all intergradations between these extremes. *Lepidopilum longifolium* often has remarkably long asexual propagula that differ from those found in most *Lepidopilum* species in their reddish brown rather than hyaline color. Its setae are long and densely spinose, and it has high-conic opercula.

Actinodontium sprucei is similar to *Lepidopilum longifolium* in plant color, and both species have erect, evenly foliate or weakly complanate-foliate stems. In addition, they have similarly shaped leaves with tightly recurved margins and nearly identical apices. Indeed, their gametophytes are so similar that *A. sprucei* can be distinguished gametophytically from *L. longifolium* only by degree: leaf apices shorter, more broadly acuminate; leaf margins more strongly recurved; and costae longer (1/3–2/3 the leaf length). *Actinodontium sprucei* consistently differs from *L. longifolium* in having setae that are smooth or somewhat roughened below the capsule and naked calyptrae.

There is an especially troubling Costa Rican collection (*Stevens 13809*, MO) of *Lepidopilum longifolium* that has short, broadly acuminate leaves, entirely revolute margins, and long costae. This collection is assigned to *L. longifolium* rather than *Actinodontium sprucei* on the basis of its numerous asexual propagula that are often densely clustered on filiform-attenuate branch and stem tips. However, the aberrant Costa Rican collection also has dense, pinnately branched rhizoids; typically *L. longifolium* has sparse, irregularly branched rhizoids. This odd collection may represent a new species.

Lepidopilum amplirete and *L. surinamensis* are somewhat similar to *L. longifolium* in having evenly foliate stems and symmetrical, often oblong, elimbate leaves. They differ from *L. longifolium* in having short-acuminate to cuspidate leaves with plane margins and shorter apical cells. In addition, they have papillose or somewhat roughened rather than spinose setae. *Lepidopilum surinamensis* further differs in its short setae (2.5–3.0 mm long). *Lepidopilum muelleri* is usually distinct from *L. longifolium* in having complanate-foliate stems and well-spaced, falcate to falcate-sigmoid lateral leaves. There is, however, a form of *L. muelleri* especially common in western Panama that is very difficult to distinguish from *L. longifolium*. This form has evenly foliate stems with closely spaced, symmetric leaves; the sporophytes of both taxa are identical in all respects. The odd form of *L. muelleri* differs from *L. longifolium* in having lanceolate leaves with sharply serrate, mostly plane margins and piliferous apices. The typical form of *L. longifolium* is well separated from the *L. muelleri*-form by its oblong or oblong-lanceolate leaves with broadly acuminate, often reflexed-recurved apices and more strongly recurved, entire to serrulate margins. There are, however, many collections of *L. longifolium* from the Caribbean and South America that intergrade with this form of *L. muelleri*.

10. *Lepidopilum muelleri* (Hampe) Hampe, Ann. Sci. Nat., Bot., sér. 5, 4: 365. 1865. *Hookeria muelleri* Hampe, Linnaea 20: 84. 1847. Protologue. [Venezuela] In Columbia [sic], aliis (*No. 119*?) intermixtam muscis Moritzii invenit C. Müller et mecum communicavit.

Hookeria deppeana Müll. Hal., Syn. Musc. Frond. 2: 196. 1851. *Lepidopilum deppeanum* (Müll. Hal.) Mitt., J. Linn. Soc., Bot. 12: 383. 1869. Protologue. Mexico: *Deppe*.

Lepidopilum floresianum Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32(1): 194. 1894. Protologue. [Costa Rica] Forêts du Rancho Flores (*Pitt*[*ier*] *n*^{o} *5659*), *syn. nov.*

Hookeria haplociliata Müll. Hal., Bull. Herb. Boissier 5: 206. 1897. *Lepidopilum haplociliatum* (Müll. Hal.) Paris, Index Bryol. Suppl. 223. 1900. Protologue. Guatemala, Coban, 4400 ped. alt., Decbr. 1885: *v. Türckheim* in Hb. *Brotheri* 1891; Alta Vera Paz, Pansamalá, 3800 ped. alt.: idem in Hb. *Levier*.

Lepidopilum pringlei Cardot, Rev. Bryol. 37: 51. 1910. Protologue. [Mexico] État de Vera-Cruz: près de Jalapa, troncs d'arbres, 1908 ([*Pringle*] *n*^{os} *10499, 15167*). Type. Plantae Mexicanae. Vera Cruz. On small trees in a dark forest near Jalapa, 4,000 ft., 25 June, 1908. *C. G. Pringle 10499* (FH, MO, syntypes), *syn. nov.*

Lepidopilum crassisetum R. S. Williams, Bryologist 27: 42. 1924. Protologue. Cocos Island, [*Alban Stewart*] *1413*. Type. California Academy of Sciences Expedition to the Galapagos Islands 1905–1906. Cocos Island. Coll: *Alban Stewart 1413* (NY, holotype), *syn. nov*.

Plants medium-sized to robust, 3–6 cm long, glossy, dark green, green, yellowish green, or reddish, in lax tufts. Primary stems prostrate and creeping. Secondary stems erect-ascending or pendent, sparsely and irregularly branched, hyaline to yellowish when young, becoming reddish with age, strongly or loosely complanate-foliate; stems in cross section with well-developed hyalodermis, 1–3 layers of small, thick-walled subepidermal cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong, hyaline; rhizoids on primary stems and at base of secondary stems, from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves distantly or closely spaced, strongly or weakly dimorphic, strongly or loosely flattened. Lateral leaves erect-spreading to wide-spreading, flat or sometimes crispate when dry, erect-spreading to falcate-spreading when wet, oblong-lanceolate, ovate-lanceolate, or lanceolate, 2.5–4.0 mm long, asymmetric or symmetric, straight or falcate, broadly to narrowly long-acuminate; margins serrulate to serrate, at times sharply serrate above, plane, sometimes narrowly recurved at base, often broadly infolded on one side at base, elimbate; costae double, slender, 1/4–1/3 the leaf length, diverging throughout, smooth at back, not projecting at the apex; cells smooth, upper cells linear, linear-fusiform, or linear-rhomboidal, 75–110 × 5–12 µm, thin-walled, not porose, becoming oblong-rectangular to oblong-fusiform below; alar cells not differentiated. Dorsal leaves at times erect to appressed, ovate to ovate-lanceolate, 2–3 mm long, symmetric. Asexual reproduction by deciduous leaves or fusiform, multicellular, uniseriate, propagula from clusters of initials abaxial to the leaf insertions at base of costae. Autoicous or synoicous. Setae elongate, 5–13 mm long, red to reddish orange, densely papillose to spinose throughout, rarely lightly papillose or smooth below and lightly papillose above. Capsules erect to suberect, oblong-cylindrical, 1–2 mm long, neck well developed; exothecial cells reddish, oblate in 3–4 rows at mouth, those below oblong to rounded-rectangular, thick-walled, somewhat collenchymatous; stomata rudimentary, 2–4-celled, on neck; opercula high-conic, 1.0–1.5 mm long; annuli of 15–25 rows of thin-walled cells, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome very narrowly triangular, median furrow absent, dorsal (outer) surface broad, whitish yellow, densely papillose throughout, trabeculae thin, median lines faint, ventral (inner) surface narrow, 1/3 or less the width of the dorsal surface, red, lightly papillose, deposition thick; endostome as long or longer than the exostome, pale yellowish, papillose throughout, basal membranes high, segments broad, concave-keeled, not perforate, cilia absent. Spores rounded, 10–16 µm, smooth to lightly papillose. Calyptrae campanulate-mitrate, 1.5–2.5 mm long, reddish yellow, irregularly lobed at base, scabrous above, often with many multicellular ramenta.

Illustrations. Williams (1924, Pl. 8); Bartram (1949, Fig. 138 A–C, as *L. haplociliatum*); Welch (1966, Figs. 199–206, as *L. deppeanum*; Figs. 248–256, as *L. pringlei*); Welch (1974, Figs. 326–337, as *L. floresianum*; Figs. 338–347, as *L. haplociliatum*); Sharp *et al.* (1994, Fig. 608, as *L. haplociliatum*; Fig. 609, as *L. pringlei*); Vaz and Costa (2006b, Figs. 44–52). Figure 196.

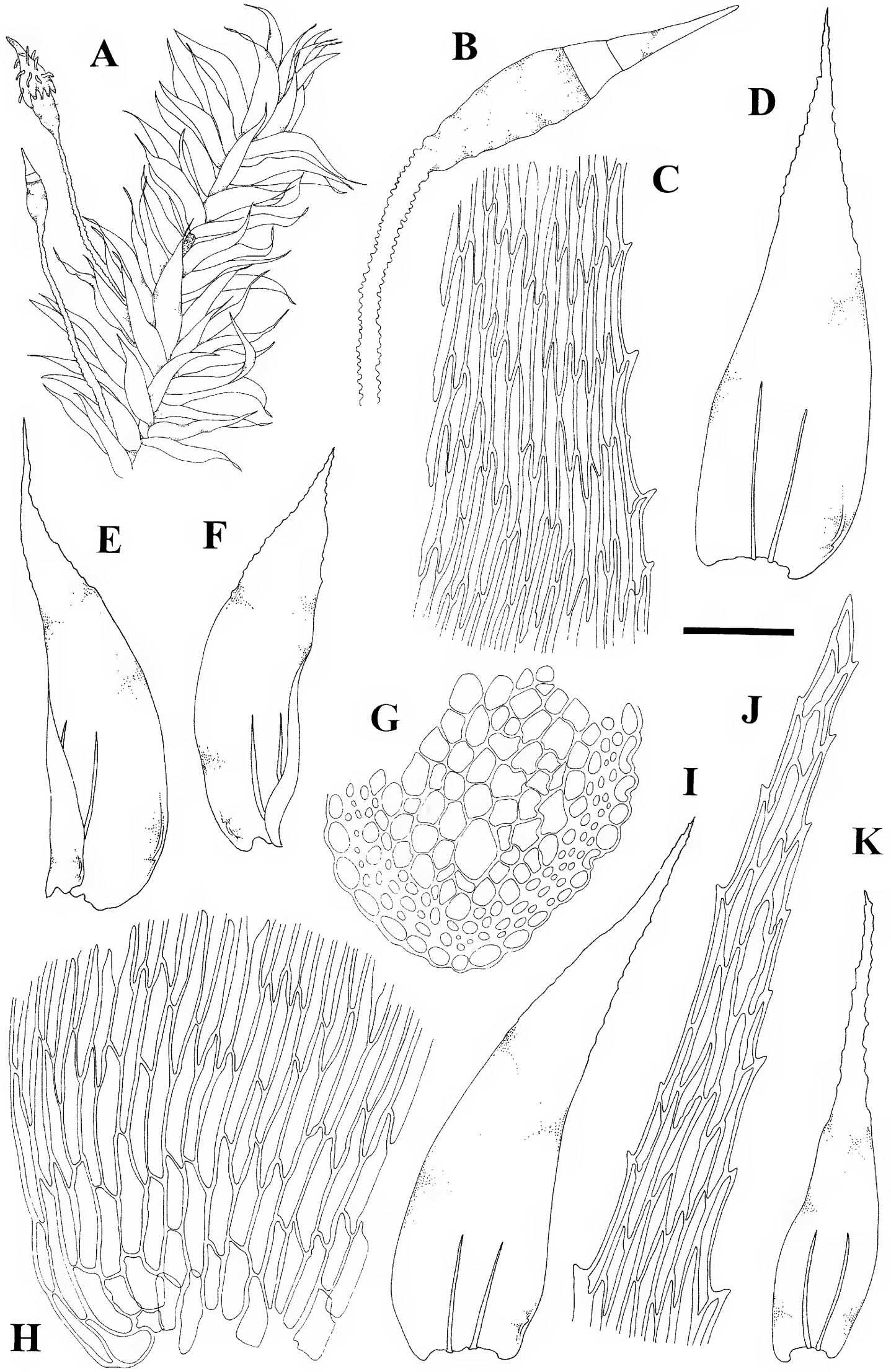


Figure 196. *Lepidopilum muelleri*. A. Habit. B. Seta, capsule, annulus, and operculum. C. Median leaf cells and margin. D–F, I & K. Leaves. G. Stem in cross section. H. Basal and alar cells. J. Leaf apex. Scale in mm: bar = 0.09 (C, H, J); bar = 0.13 (G); bar = 0.7 (B, D–F, I, K); bar = 3.2 (A). A, B, G from *Allen 11245*; E from *Stewart 1413* (type *L. crassisetum*); F from *Pringle 10499* (type *L. pringlei*); all other figure parts from *Allen 5733*.

Habitat. On twigs, fern rachis, leaves, festooning small stems, small branches, tree trunks, logs, and roots; 50–3200 m.

Distribution in Central America. BELIZE: Toledo: *Allen 18675* (MO). GUATEMALA. Alta Verapaz: *Standley 91485* (F, FH); San Marcos: *Standley 86548b* (F, FH). EL SALVADOR. Santa Ana: *Watson ES-0033* (MO); Sonsonate: *Kovar 1* (NY). HONDURAS. Comayagua: *Allen 13866* (MO, NY, TEFH, US); Cortés: *Allen 14380* (MO, NY, TEFH); Francisco Morazán: *Richards et al. 3590* (F, MO); Lempira: *Allen 11379* (MO, TEFH); Ocotepeque: *Allen 14450A* (MO); Santa Bárbara: *Allen 11694* (MO, TEFH); Yoro: *Allen 13666* (MO). COSTA RICA. Alajuela: *Crosby & Crosby 5901* (MO); Cartago: *Crosby & Crosby 5792* (MO); Guanacaste: *Dauphin et al. 1915* (MO); Heredia: *Crosby & Crosby 6002* (MO); Limón: *Standley 36569a* (FH, US); Puntarenas: *Gómez et al. 21826* (MO), Cocos Island: *Svenson 347* (FH, NY); San José: *Crosby & Crosby 5892* (CR, MO). PANAMA. Bocas del Toro: *Allen 5733* (MO, PMA); Chiriquí: *McPherson 7250A* (MO); Coclé: *McPherson 7694H* (MO); Colón: *Crosby 10450* (MO); Panamá: *Crosby 10416* (MO); Veraguas: *Crosby 10149* (MO).

World range: Mexico; Central America; Caribbean; Western and Northern South America.

Lepidopilum muelleri is a fairly common species in Central America. It is usually an epiphyte, often collected on twigs. The species can have closely or distantly spaced leaves that are usually dimorphic: lateral leaves oblong-lanceolate, ovate-lanceolate, or lanceolate, complanate-flattened, asymmetric; dorsal leaves ovate to ovate-lanceolate, symmetric, erect to appressed, symmetric. There are, however, many collections from western Panama that have evenly foliate stems with monomorphic, symmetric, ovate-lanceolate or lanceolate leaves rather than complanate-foliate stems. The leaves in *L. muelleri* have long-acuminate, at times nearly piliferous apices; elimbate, sharply serrate to serrulate margins; thin-walled, linear, linear-fusiform, or linear-rhomboidal cells; and typically short, weak costae that often end below midleaf. Even though *L. muelleri* is autoicous or synoicous and collections regularly have sporophytes, its plants often reproduce asexually by means of uniseriate propagula clustered at the base of the leaves. In addition, plants of *L. muelleri* from Cocos Island have deciduous leaves identical to those often present in *L. scabrisetum*. The setae of *L. muelleri* are nearly always spinose-papillose throughout and typically long. However, setae length varies considerably in the species, and occasionally collections have lightly papillose setae (*e.g.*, *Gómez et al. 21826*, MO) or setae smooth in the lower two-thirds and lightly papillose above (*e.g.*, *Knapp 1564*, MO). The calyptrae typically are densely beset with multicellular ramenta.

In Central America *L. muelleri* will most likely be confused with those *Lepidopilum* species that have complanate-foliate stems and elimbate, falcate leaves: *L. brevipes*, *L. cuspidans*, and *L. scabrisetum*. Most collections of *L. brevipes* and *L. cuspidans* are more slender than *L. muelleri*, and they usually have shorter (2–3 mm vs. 2.5–4.0 mm) leaves. They also differ from *L. muelleri* in having shorter setae (1.0–3.5 mm vs. 5–13 mm). In addition, *L. brevipes* has mostly naked calyptrae. *Lepidopilum scabrisetum* differs from *L. muelleri* in having somewhat shorter, acute to short-acuminate leaves. These two species are gametophytically very close, and Buck (1998) considered all West Indian material previously named *L. muelleri* to fall within his concept of *L. scabrisetum.* However, at least one collection from Dominica (*Elliott 26a*, FH) agrees with the concept of *L. muelleri* used here.

The extreme western Panama expression of *L. muelleri* noted above with evenly foliate stems and symmetric leaves (*e.g.*, *Allen 5691, 5728, 5765, 5768*, all MO) can be difficult to distinguish from *L. longifolium*. That species differs from this form of *L. muelleri* in having oblong-oval, oblong, or oblong-lanceolate leaves with narrowly recurved margins that are entire to weakly serrulate and gradually, broadly acuminate apices that are often reflexed-recurved when dry. In addition the upper leaf cells of *L. longifolium* are usually broader (10–17 µm vs. 5–12 µm) than those of *L. muelleri*.

11. *Lepidopilum pallidonitens* (Müll. Hal.) Paris, Index Bryol. Suppl. 223. 1900. *Hookeria pallidonitens* Müll. Hal., Nuovo Giorn. Bot. Ital., n. ser. 4: 132. 1897. Protologue. Bolivia. Locality and collector not given. Type (see Churchill 1988). Bolivia. Cochabamba, prope Choquecamata, Jun 1889, *Germain s.n.* (NY, isotype).

Lepidopilum quadrifarium Herzog, Beih. Bot. Centralbl., Abt. 2, 61: 589. 1942. Protologue. Costa Rica: La Palma, 1500 m, leg. *M. Valerio* (*no. 45*).

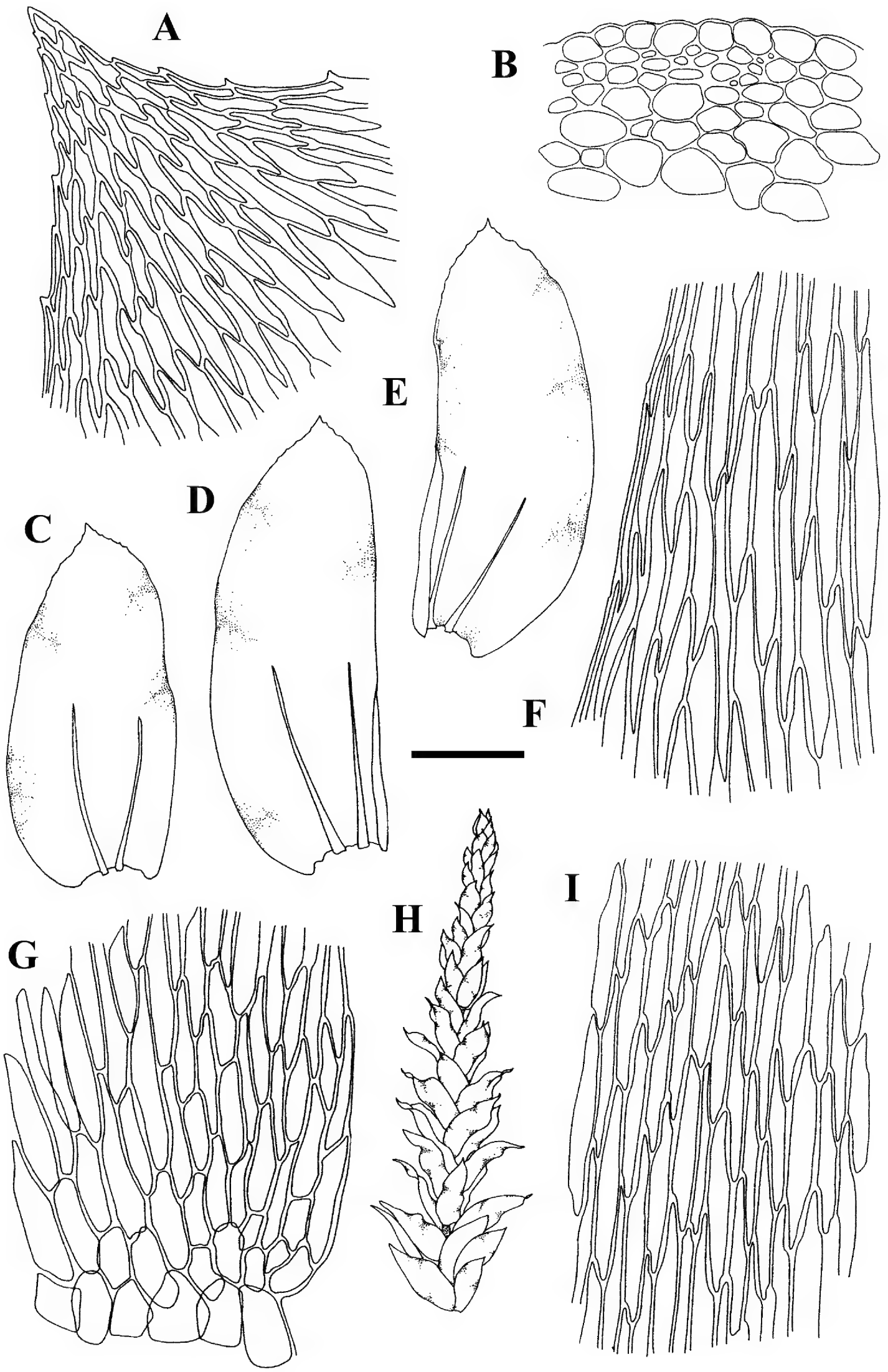
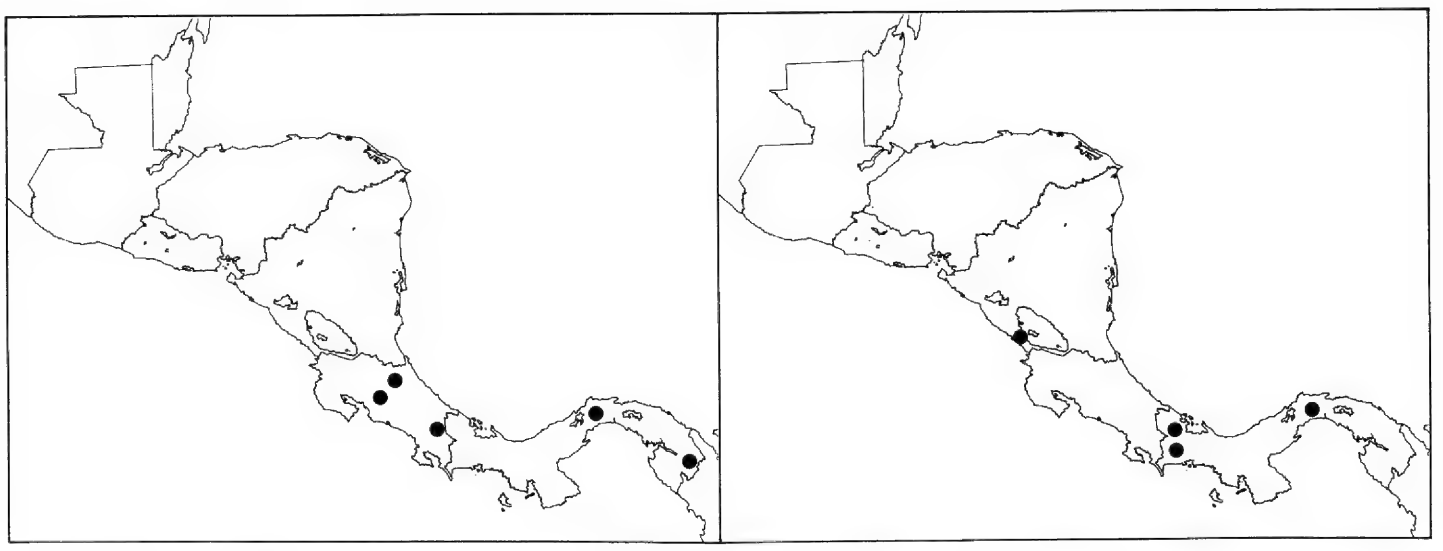


Figure 197. *Lepidopilum pallidonitens*. A. Leaf apex. B. Stem in cross section. C. Dorsal leaf. D & E. Lateral leaves. F. Median leaf cells and margin. G. Basal and alar cells. H. Habit. I. Median leaf cells. Scale in mm: bar = 0.09 (A, F, G, I); bar = 0.13 (B); bar = 0.9 (C–E); bar = 2.5 (H). All figure parts from *Crosby 6071*.



Lepidopilum pallidonitens *Lepidopilum permarginatum*

Lepidopilum attenuatum E. B. Bartram, Rev. Bryol. Lichénol. 33: 11. 1964. Protologue. [Ecuador] On outcropping rocks and tree bases, Shinguipino rain forest, 8 km S.E. of Tena, c. 1500 ft., [*Peter J. Grubb*] *2939a*. Types. Flora of Ecuador. Cerro Antisana (lat. 0°30′S : long. 78°W). On outcropping rocks and tree bases, Shinguipuri [sic], rain forest 8 km S.E. of Tena, alt. c. 1500 ft., 27.9.1960, *P. J. Grubb 2939a* (FH, holotype; FH, isotype), *syn. nov.*

Plants medium-sized, 2–3 cm long, glossy, green, yellowish green, or reddish yellow. Primary stems prostrate and creeping. Secondary stems prostrate or ascending, not or sparsely branched, hyaline to yellowish when young, becoming red to red brown with age, often attenuate-foliate at tips; stems in cross section with well-developed hyalodermis, 2–3 layers of small, thick-walled subepidermal cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong, hyaline; rhizoids on primary stems and secondary stems, from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves closely spaced, strongly complanate, weakly dimorphic. Lateral leaves erect-spreading to spreading when wet, spreading, plane or lightly crispate when dry, oblong to oblong-ovate, 2–3 mm long, weakly asymmetric, obtuse to broadly acuminate, apiculate; margins entire below, serrulate above, elimbate, plane above, broadly infolded on one side at base; costae double, weak, 1/3–1/2 the leaf length, diverging throughout, smooth at back, not projecting at the apices; cells smooth, median cells linear-fusiform to long-fusiform, 100–180 × 8–18 µm, thin-walled, not porose, lower cells elongate-rectangular, thin-walled, not porose, cells across the base enlarged, subrectangular; alar cells not differentiated. Dorsal leaves erect to appressed when wet, oblong to obovate, symmetric; margins entire below, serrulate above, elimbate, plane. Asexual propagula fusiform, multicellular, uniseriate, arising from clusters of initials abaxial to the leaf insertions at base of costae. Dioicous. Sporophytes not seen, description from Churchill (1988). Setae elongate, 6–9 mm long, yellowish red, papillose and spinose throughout. Capsules suberect, ovoid-cylindrical, to 1.6 mm long; opercula conic rostrate. Calyptrae campanulate-mitrate, 2.2–2.4 mm long, with multicellular ramenta.

Illustrations. Herzog (1942, Fig. 18); Churchill (1988, Figs. 23 & 24); Churchill (1994, Fig. 12 A & B). Figure 197.

Habitat. On moist banks, rocks, tree bases, and twigs; 300–1000 m.

Distribution in Central America. COSTA RICA. Heredia: *Crosby & Crosby 6016* (CR, MO); Puntarenas: *Palmer L3* (FH, MO, NY); San José: *Valerio 45* (JE). PANAMA. Darién: *Allen 8995* (MO); Panamá: *Crosby 10091* (MO).

World range: Central America; Western South America.

Lepidopilum pallidonitens is a medium-sized species with glossy, yellowish green plants and strongly complanate-foliate stems. South American plants of *L. pallidonitens* have distinctly flattened

leaves, which give the plants an aspect similar to *Homalia glabella* or *Crossomitrium rotundifolium*. Plants from Central America, however, have leaves that are somewhat flexuose when dry. *Lepidopilum pallidonitens* has asymmetric, oblong to oblong-ovate, obtuse to broadly acuminate lateral leaves; thin-walled, linear-fusiform to long-fusiform upper cells; short, faint, costae that usually end below midleaf; and serrulate upper margins. The marginal leaf cells are much thinner and somewhat longer than the median leaf cells, but the leaves are not obviously bordered since the cells become gradually narrower toward the margins. A distinctive and diagnostic feature of *L. pallidonitens* is the frequent presence of long, attenuate-foliate stem tips.

In Central America the combination of flattened plants and asymmetric, falcate lateral leaves gives *Lepidopilum pallidonitens* an aspect also encountered in *L. muelleri*, *L. brevipes*, *L. scabrisetum*, and *L. diaphanum.* All four species differ from *L. pallidonitens* in having narrower, short- to long-acuminate leaves and in lacking attenuate-foliate stem tips. *Lepidopilum diaphanum* further differs in having border leaves with costae 1/3–2/3 the leaf length and very broad (30–50 µm wide) hexagonal to rhomboidal median leaf cells. *Lepidopilum pallidonitens* and *L. affine* are also similar in having rounded to obtuse leaf apices. However, in *L. affine* the narrower, ovate-oblong to oblong-lingulate, symmetric leaves have sharply serrate upper margins that are strongly undulate to crispate when dry.

12. *Lepidopilum permarginatum* R. S. Williams, Bryologist 28: 60. 1925. Protologue. Cordoba, Department of El Valle, Colombia. *E. P. Killip*, Oct., 1922, *11794*; also from Buenaventura, same Department and Collector, *11767*. Types. Exploration in Colombia, Department of El Valle, Cordoba, Dagua Valley, forest along Rio Calima, Alt 80–100 m, *Ellsworth P. Killip 11794*, October 9, 1922 (MO, syntype); Exploration in Colombia, Department of El Valle, Buenaventura, Pacific Coast, Alt 0–10 m, *Ellsworth P. Killip 11767*, October 5–10, 1922 (MO, syntype).

Plants medium-sized to robust, 3–6 cm long, dark green, greenish yellow, or reddish yellow, in lax tufts. Primary stems prostrate and creeping. Secondary stems erect or ascending, not or sparsely branched, hyaline to yellowish when young, becoming red to red brown with age, evenly foliate; stems in cross section with hyalodermis, 1–3 layers of small, thick-walled subepidermal cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong, hyaline; rhizoids usually on primary stems and at base of secondary stems, from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves more or less distant, not or weakly dimorphic, flexuose-contorted when dry, loosely erect-spreading when wet, broadly oblong, 4–5 mm long, symmetric, short- to long-acuminate, often twisted; margins serrulate near base, serrate to spinose above, often doubly serrate, plane or broadly incurved on one side below, limbate, border strongly developed, of 4–8 rows of elongate cells; costae double, strong, ending 2/3–3/4 the leaf length, often red, diverging throughout, smooth at back, not projecting at the apices, at times one fork merging with the leaf border; cells smooth, usually porose, median cells long-rhomboidal to hexagonal, 35–60 × 18–25 µm, thin-walled, lower cells rectangular; alar cells not differentiated. Asexual propagula fusiform, multicellular, uniseriate, arising from clusters of initials abaxial to the leaf insertions at base of costae. Dioicous. Sporophytes not known in Central America and not seen, description from Williams (1925) and Churchill (1988). Setae elongate, 11–14 mm long, reddish orange, spinose or papillose throughout. Capsules erect, ovoid or short-oblong, 1.1–1.3 mm long; exothecial cells short-oblong to rectangular; opercula conic-apiculate or conic short-rostrate, 1.0–1.2 mm long; peristome diplolepideous, exostome narrowly lanceolate, papillose throughout; endostome as long as the exostome, lightly papillose throughout, basal membranes short, cilia absent. Spores 12–16 µm, minutely papillose. Calyptrae campanulate-mitrate, 3 mm long, scabrous above, laciniate at base, usually with few multicellular ramenta.

Illustrations. Churchill (1988, Fig. 41). Figure 198.

Habitat. On rocks, tree bases, and rotting logs; 850–1190 m.

Distribution in Central America. NICARAGUA. Rivas: *Granzow de la Cerda & Moreno 1685* (NY). PANAMA. Bocas del Toro: *Allen 5623* (MO); Chiriquí: *Salazar 5556* (MO); Panamá: *Crosby 10916* (CR, DUKE, F, FH, MO, NY, PMA, US).

World range: Central America; Western South America.

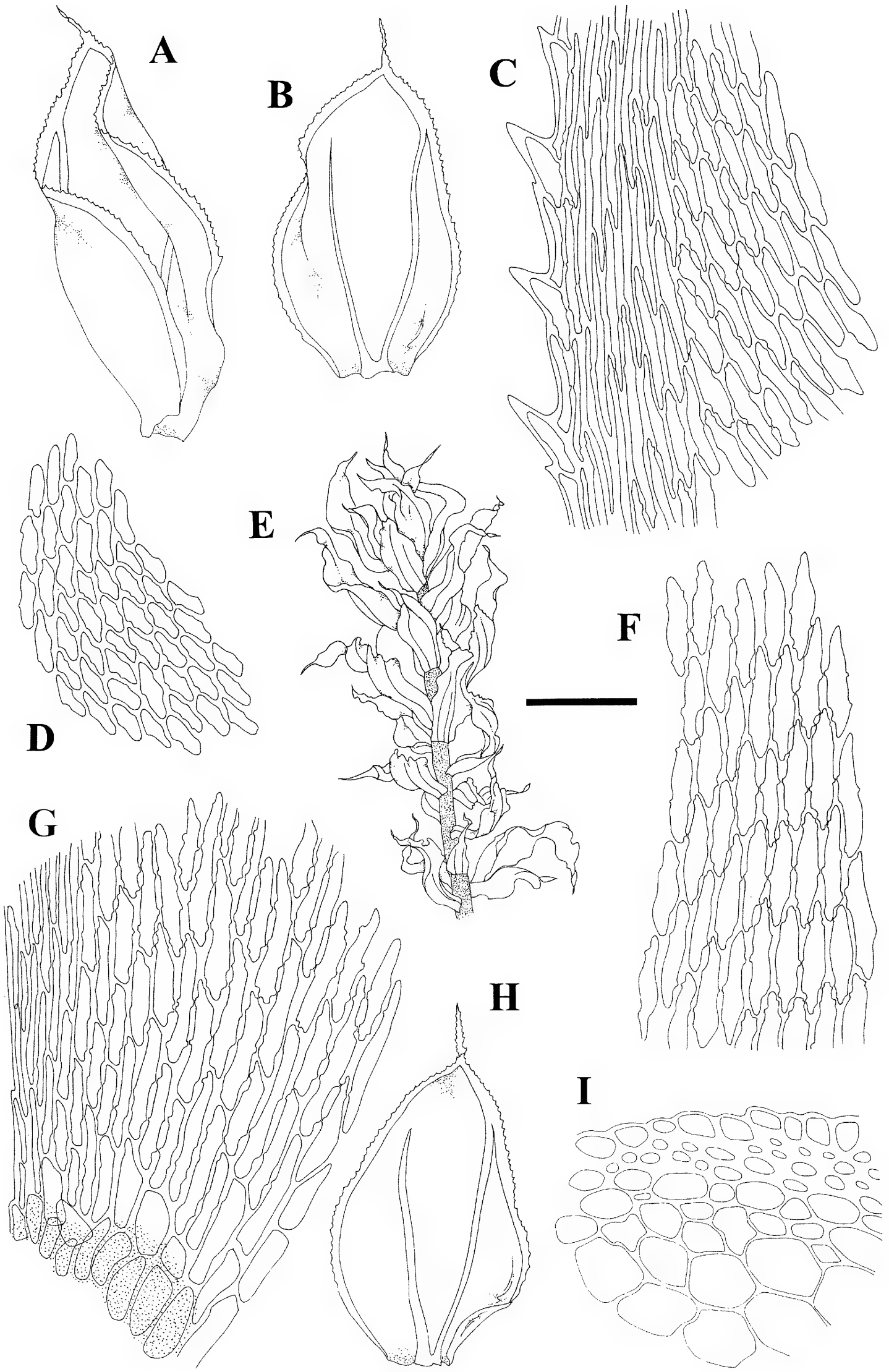


Figure 198. *Lepidopilum permarginatum*. A, B & H. Leaves. C. Upper leaf cells and margin. D. Median leaf cells. E. Habit. F. Lower leaf cells. G. Basal and alar cells. I. Stem in cross section. Scale in mm: bar = 0.08 (I); bar = 0.09 (C, D, F); bar = 0.13 (G); bar = 1.25 (A, B, H); bar = 2.5 (E). All figure parts from *Crosby 10916*.

Lepidopilum permarginatum is a medium-sized to robust species with large, broadly oblong leaves, 4–5 mm long. When dry or wet the plants typically have flexuose-contorted leaves that are usually twisted above. Its leaves are symmetric and not or weakly dimorphic. The most distinctive feature of *L. permarginatum* is its strongly developed leaf borders that can be eight cells wide and often completely fill the leaf apices. *Lepidopilum permarginatum* leaves have rhomboidal to hexagonal upper cells and well-developed, stout costae that end near the apex. In most leaves one fork of the costae merges above with the leaf border. *Lepidopilum permarginatum* is usually dioicous, and sporophytes are unknown from Central America. Collections of the species from Colombia have long setae that are spinose or papillose throughout.

In Central America *Lepidopilum permarginatum* is likely to be confused only with *L. polytrichoides* because both are large species with similarly shaped leaves that have sharply serrate margins and an identical leaf areolation. Most collections of *L. polytrichoides* differ from *L. permarginatum* in having longer leaves (to 8 mm long) that are weakly bordered (1–3 rows of linear cells) and have short (1/3 the leaf length), weak costae. In addition, *L. polytrichoides* is synoicous and its plants often have short setae (2–4 mm long). There is, however, a puzzling form of *L. polytrichoides* in Central America with medium-sized plants and strongly bordered (4–5 rows of linear cells) leaves. In addition, this form of *L. polytrichoides* also has leaves with well-developed, long (at times 3/4 the leaf length) costae that sometimes have one fork merged with the leaf border. When sporophytes are absent this form is extremely difficult to distinguish from *L. permarginatum*.

13. *Lepidopilum polytrichoides* (Hedw.) Brid., Bryol. Univ. 2: 269. 1827. *Hypnum polytrichoides* Hedw., Sp. Musc. Frond. 244. 1801. *Orthotrichum polytrichoides* (Hedw.) Brid., Muscol. Recent. 2(2): 31. 1801. *Neckera polytrichoides* (Hedw.) Sw., Fl. Ind. Occid. 3: 1794. 1806. *Pilotrichum polytrichoides* (Hedw.) Brid., Muscol. Recent. Suppl. 4: 140. 1819. *Daltonia polytrichoides* (Hedw.) Arn., Mém. Soc. Hist. Nat. Paris 2: 303. 1826. *Hookeria polytrichoides* (Hedw.) Spreng., Syst. Veg. 4: 197. 1827. Protologue. Jamaica [*Swartz*].

Lepidopilum excelsum Müll. Hal., Flora 58: 547. 1874. Protologue. [Colombia] Nova Granata, prov. Antioquia, Rio verde, 6000′, Frontino 8000′: *G. Wallis* 1874.

Lepidopilum polytrichoides (Hedw.) Brid var. *pellucens* Besch., Ann. Sci. Nat., Bot., sér. 6, 3: 231. 1876. Protologue. Guadeloupe (*L'Herminier*).

Lepidopilum subpolytrichoides Müll. Hal., Linnaea 42: 495. 1879. Protologue. Venezuela, [1855, *Fendler*, Nr. 123]. Type. Musci Fendleriani Venezuelenses *123* (FH, isotype).

Lepidopilum platyphyllum Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32(1): 192. 1894. Protologue. [Costa Rica] Bois de la vallée du Rio Tuis, bassin du Reventazon, 600 m. (*Pitt*[ier] *n° 5656*). Types. Plantae costaricenses exsiccatae. *N° 5656.* Bois de la vallei du Rio Tuis, Bassin du Reventazon, 600 m, September 1893, legit H. Pittier, *Tonduz* (US, isotype); Costa Rica, bois du Rio Tuis, alt. 600 ^{m} leg. *Tonduz*, 1893 (NY, isotype).

Lepidopilum polytrichoides (Hedw.) Brid. var. *costa-ricense* Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32(1): 192. 1894. Protologue. [Costa Rica] Buenos Aires, (*Pitt*[ier] *n° 5654*). Forêts du Rio Naranjo, 200–2501 m. ([Pittier] *n° 5655*). Type. Plantae costaricenses exsiccatae. *N° 5654.* Buenos Aires, 1891, *legit H. Pittier* (US, syntype).

Lepidopilum mnioides Müll. Hal., Flora 83: 337. 1897. Protologue: Venezuela, Tovar Caracas altitudine ca. 3000 ped. [*C. Goebel*].

Hookeria carionis Müll. Hal., Bull. Herb. Boissier 5: 205. 1897. *Lepidopilum carionis* (Müll. Hal.) Paris, Index Bryol. Suppl. 221. 1900. Protologue. [Guatemala] In sylvis primaevis ad arbores pr. Sa Cruz Almor, Sept. 1876. [*Bernoulli & Cario*] Col. *N° 65.*

Plants medium-sized to robust, 3–10 cm long, light to dark green, greenish yellow, occasionally reddish, in lax tufts. Primary stems prostrate and creeping. Secondary stems erect or ascending, not or sparsely branched, hyaline to yellowish when young, becoming red to red brown with age, usually complanate-foliate; stems in cross section with hyalodermis, 1–2 layers of small, thick-walled subepidermal cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong, hyaline; rhizoids usually on primary stems and at base of secondary stems, from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves more or less distant, usually flattened, variously dimorphic, contorted-

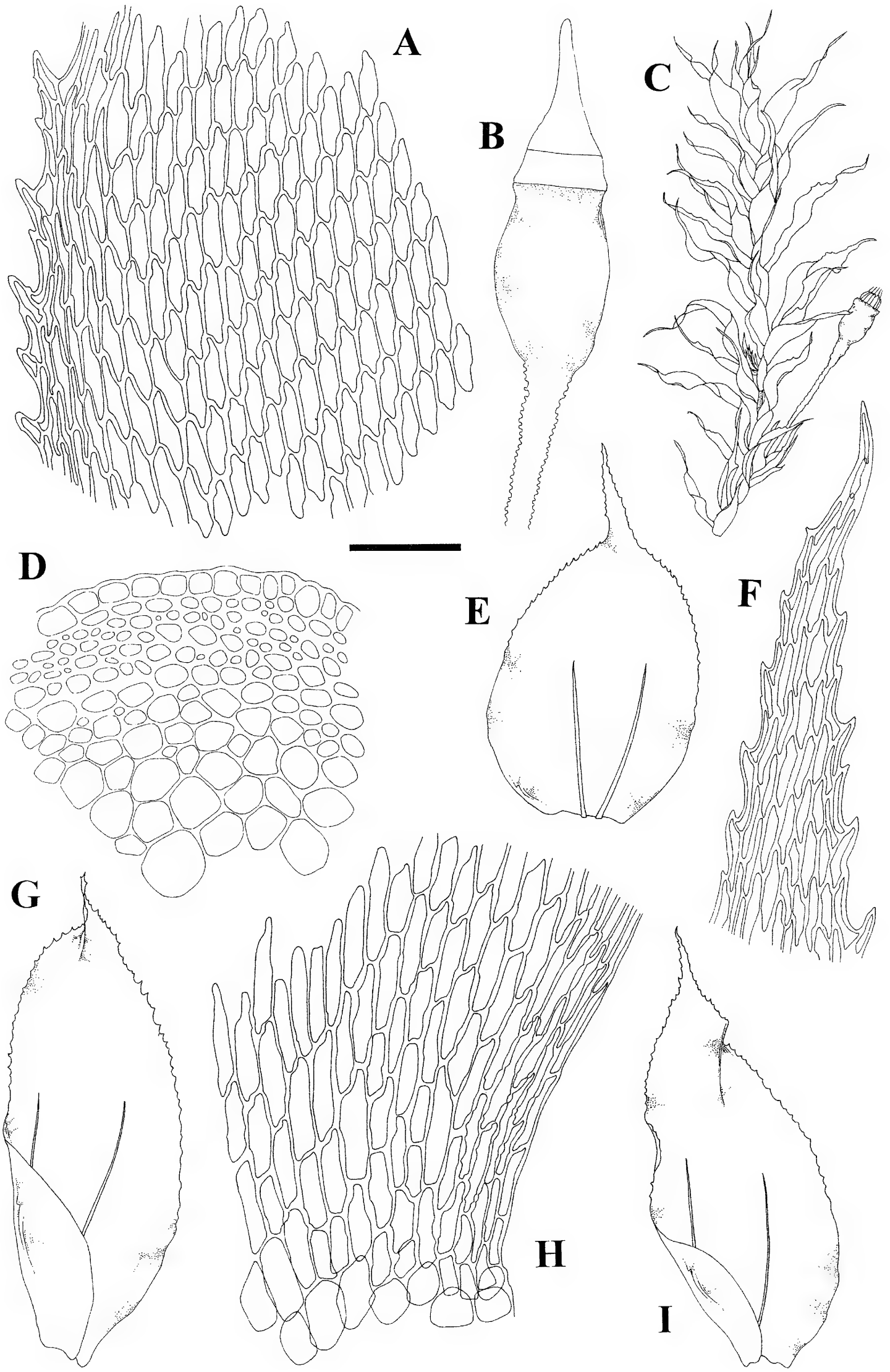
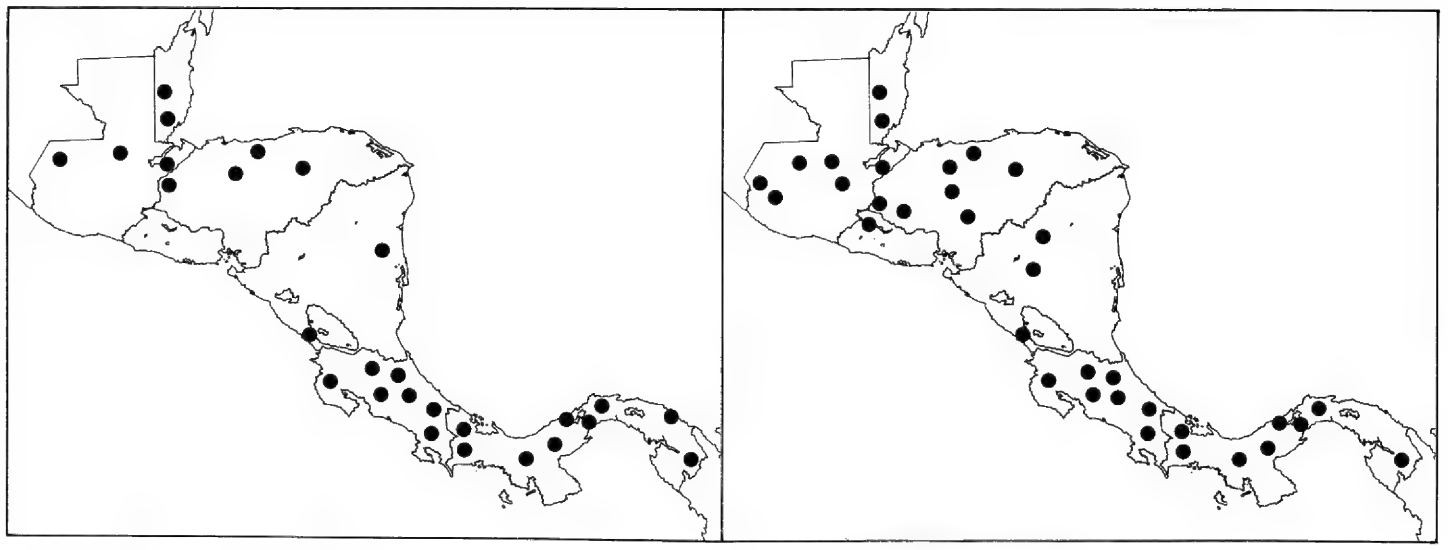


Figure 199. *Lepidopilum polytrichoides*. A. Upper leaf cells and margin. B. Seta, capsule, annulus, and operculum. C. Habit. D. Stem in cross section. E. Dorsal leaf. F. Leaf apex. G & I. Lateral leaves. H. Basal and alar cells. Scale in mm: bar = 0.08 (D); bar = 0.13 (A, F, H); bar = 0.6 (B); bar = 1.25 (E, G, I); bar = 2.5 (C). B, C from *Crosby 10851*; all other figure parts from *Allen 18357*.



Lepidopilum polytrichoides *Lepidopilum scabrisetum*

crispate when dry. Lateral leaves erect- to wide-spreading when wet, ovate-lanceolate to ovate-oblong, 3.5–8.0 mm long, asymmetric, short- to long-acuminate, often twisted; margins serrate to spinose above, limbate, border weak or well developed by 2–4(–5) rows of elongate cells, plane above, broadly infolded on one side at base; costae double, slender, ending 1/3–2/3(–3/4) the leaf length, diverging throughout, smooth at back, not projecting at the apices; cells smooth, median cells rhomboidal to hexagonal, 75–120 × 28–34 µm, thin-walled, lower cells rectangular; alar cells not differentiated. Dorsal leaves erect when wet, ovate, broadly ovate-lanceolate, to oblong-ovate, 3–6 mm long, symmetric, short- to long-acuminate, margins serrate to spinose above, limbate, border weak or well developed by 2–4(–5) rows of elongate cells, plane. Synoicous, autoicous, or dioicous. Setae short, 2–4 mm long, yellow when young, becoming red to reddish orange with age, densely papillose above and roughened below or papillose throughout. Capsules erect, ovoid to oblong-cylindrical, 1–2 mm long, neck weakly developed; exothecial cells reddish, oblate in 2–3 rows at mouth, those below oblong to rectangular, firm-walled, not or obscurely collenchymatous; stomata rudimentary, 3–6-celled, on neck; opercula high-conic, 0.7–1.0 mm long; annuli of 7–9 rows of thin-walled cells, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome very narrowly triangular, median furrow absent, dorsal (outer) surface broad, whitish yellow, lightly papillose throughout, trabeculae thin, median lines faint, ventral (inner) surface narrow, 1/3 or less the width of the dorsal surface, dark red, lightly papillose, deposition thick; endostome as long as the exostome, pale yellowish, lightly papillose throughout, basal membranes high, segments broad, concave-keeled, not perforate, cilia absent. Spores rounded, 10–16 µm, smooth to lightly papillose. Calyptrae campanulate-mitrate, 1.5–2.0 mm long, reddish yellow, irregularly lobed at base, scabrous, usually with few to many multicellular ramenta.

Illustrations. Hedwig (1801, Pl. 61 7–8); Brotherus (1907a, Fig. 701); Brotherus (1925, Fig. 609); Bartram (1949, Fig. 140 A–D); Welch (1962, Figs. 33–36); Breen (1963, Pl. 104); Welch (1966, Figs. 242–247); Welch (1974, Figs. 357–370, as *L. platyphyllum*); Crum and Anderson (1981, Fig. 397); Reese (1984, Fig. 45 A–C); Florschütz-de Waard (1986, Fig. 132); Churchill (1988, Fig. 48); Sharp *et al.* (1994, Fig. 600); Churchill (1994, Fig. 11 F & G); Churchill and Linares (1995, Fig. 41 h–j); Duarte Bello (1997, Pl. 231); Buck (1998, Pl. 12); Buck (2003, Fig. 95). Figure 199.

Habitat. On vines, twigs, branches, trunks of trees or treelets, buttress roots, and bare rock or karst outcrops, occasionally epiphyllous; 30–2100 m.

Distribution in Central America. BELIZE. Cayo: *Allen 18357* (BRH, MO); Toledo: *Allen 18669* (BRH, MO). GUATEMALA. Alta Verapaz: *Johnson 448* (FH, NY, US); Huehuetenango: *Steyermark 49368* (F, FH, MO); Izabal: *Steyermark 41736* (F, FH, MO, NY). HONDURAS. Atlántida: *Standley 53220* (F, FH, NY, US); Copán: *Blake 7481B* (NY, US); Olancho: *Allen 12809* (MO); Yoro: *Liesner 26681* (MO, TEFH). NICARAGUA. Rivas: *Granzow de la Cerda GC-1659* (DUKE, MO); Zelaya: *Schramm* (NY, US). COSTA RICA. Alajuela: *Gómez et al. 19104* (MO); Cartago: *Crosby & Crosby 5940* (CR, MO, NY); Guanacaste: *Standley 44698* (FH, NY, US); Heredia: *Crosby & Crosby 6609*

(CR, F, FH, MO, NY, PMA, US); Limón: *Standley 37339* (FH, NY, US); Puntarenas: *Gómez 25415* (CR, MO); San José: *Alfaro 159* (FH, US). PANAMA. Bocas del Toro: *Allen 5862* (MO, PMA, NY); Canal Area: *Killip 12150* (FH, NY, US); Chiriquí: *Folsom et al. 5536* (MO); Coclé: *Hammel 4132* (MO, NY, PMA); Colón: *Crosby 10782* (MO, PMA); Darién: *Williams 1056* (F, FH, MO, NY); Panamá: *Crosby 4362* (F, MO, NY, US); San Blas: *Sytsma et al. 2689* (MO); Veraguas: *Crosby 10851* (MO, NY, PMA, US).

World range: Southeastern U.S.A.; Mexico; Central America; Caribbean; Western and Northern South America, Brazil.

Lepidopilum polytrichoides is usually a robust species with ovate-lanceolate lateral leaves that can be 8 mm long. It has well-developed, creeping primary stems with long secondary stems that reach 10 mm in length. Dry plants usually have a distinctive aspect due to its complanate-foliate stems and rigid, crispate-contorted leaves with twisted apices, but there are occasional collections with soft leaves that are unchanged when dry. These odd collections, however, may represent a habitat-induced form, since there are collections that have some branches with typical leaves and others with soft, unchanged leaves. *Lepidopilum polytrichoides* has short- or long-acuminate, dimorphic leaves with asymmetric, ovate-lanceolate lateral leaves and symmetric broadly ovate dorsal leaves. The leaves have rhomboidal to hexagonal upper cells; thin, smooth costae that do not project at the tips and usually end at or just above midleaf (occasionally reaching 2/3 the leaf length); and serrate to spinose upper margins that are variously bordered by multiple rows of narrow, elongate, often porose cells. *Lepidopilum polytrichoides* is synoicous, autoicous, or occasionally dioicous. Since most collections have sporophytes, the apparently dioicous collections may actually be rhizoautoicous. The setae are short and either papillose above and roughened below or papillose throughout.

In Central America there is a fairly common, puzzling form of *Lepidopilum polytrichoides* with medium-sized plants that have well-spaced, short (3.5–4.0 mm long), ovate-oblong lateral leaves. The shortly acuminate leaves are strongly bordered by 4(–5) rows of linear, thick-walled cells, and their long costae sometimes reach three-quarters the leaf length. Furthermore, one fork of the costae often merges with the leaf border. The gametophytes of this form seem to represent a distinct species, but it often has sporophytes and they are identical to those of *L. polytrichoides* in all respects. When sporophytes are absent, this form is very difficult to distinguish from *L. permarginatum*.

Lepidopilum polytrichoides is the largest species of *Lepidopilum* in Central America, and when its lateral leaves are greater than 6 mm long it can be distinguished from all other members of the genus. At times *Lepidopilum surinamense*, *L. curvifolium*, and *L. permarginatum* can be confused with *L. polytrichoides* because they are large species with bordered, sharply serrate leaves and they have rhomboidal to hexagonal median leaf cells. All three species differ from *L. polytrichoides* in their consistently dioicous sexual condition. *Lepidopilum surinamense* is also similar to *L. polytrichoides* in having short setae, but it has much shorter (2.5–3.2 mm long) obovate lateral leaves. *Lepidopilum permarginatum* differs from *L. polytrichoides* in its longer setae (11–14 mm long) and leaves that are bordered by 6–8 rows of cells. *Lepidopilum curvifolium* differs from *L. polytrichoides* in having broadly ovate to ovate-oblong, short-acuminate, somewhat shorter (3.5–5.0 mm) lateral leaves.

The protologue of *Lepidopilum platyphyllum* implies Pittier collected the type, but the handwritten label on an isotype at US indicates the type was gathered by Tonduz. Pittier often issued collections made by Tonduz in his *Plantae costaricenses exsiccatae*. The collector name and number for *L. platyphyllum* in the protologue refer to the number in Pittier's exsiccatae.

14. *Lepidopilum scabrisetum* (Schwägr.) Steere, Bryologist 51: 140. 1948. *Neckera scabriseta* Schwägr., Sp. Musc. Frond., Suppl. 1(2): 153. 1816. *Pilotrichum scabrisetum* (Schwägr.) Brid., Muscol. Recent. Suppl. 4: 141. 1819 [1818]. *Daltonia scabriseta* (Schwägr.) Arn. Mém. Soc. Linn. Paris 5: 296. 1827. Protologue. [French Guiana] In arboribus Guianae lectam dedit cl. *Richard*.

Lepidopilum subenerve Brid., Bryol. Univ. 2: 268. 1827, illegitimate name, includes a species with priority. *Hookeria subenervis* (Brid.) Hampe, Linnaea 20: 84. 1847. Protologue. [French Guiana] In Guianâ ubi *Richard* detexit et [Brazil] in montibus d'Estrella Brasiliae in arboribus habitat.

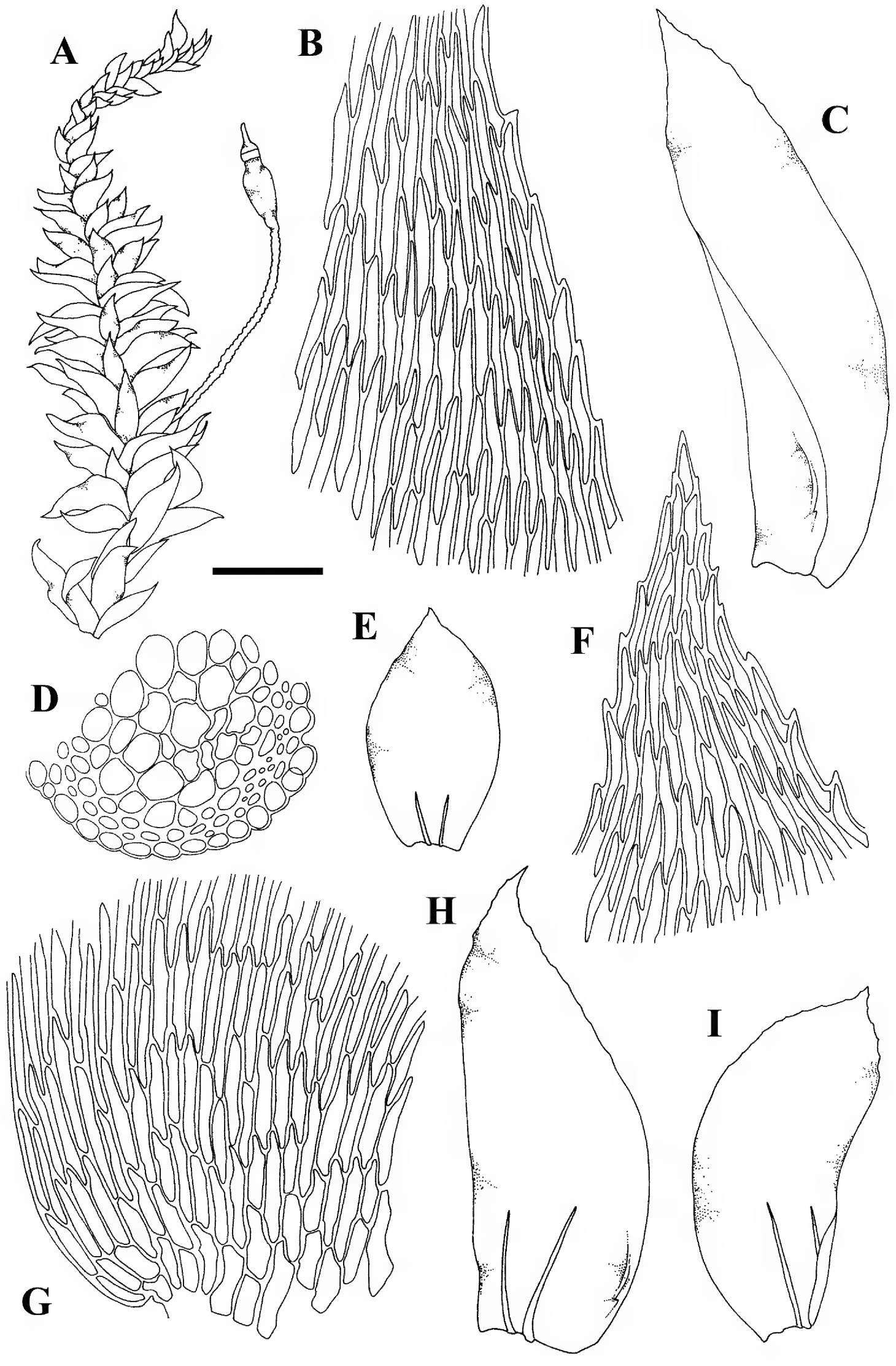


Figure 200. *Lepidopilum scabrisetum*. A. Habit. B. Upper leaf cells and margin. C & H. Leaves. D. Stem in cross section. E & I. Leaves from deciduous leaf form. F. Leaf apex. G. Basal and alar cells. Scale in mm: bar = 0.09 (B, F, G); bar = 0.13 (D); bar = 0.5 (C, E, H, I); bar = 2.0 (A). C, D, H from *Crosby 5907*; E, I from *Allen 15494*; all other figure parts from *Allen 12774*.

Trachypodium subenerve Brid., Bryol. Univ. 2: 268. 1827, invalid name, listed in synonymy.

Hookeria intermedia Müll. Hal., Syn. Musc. Frond. 2: 195. 1851. *Lepidopilum intermedium* (Müll. Hal.) Mitt., J. Linn. Soc., Bot. 12: 376. 1869. Protologue. Insula Trinidad Antillarum, ubi legit *Crüger* 12 Mart. et 28 Aug. 1847. monte Tocuche.

Hookeria latifolia Müll. Hal., Syn. Musc. Frond. 2: 199. 1851. *Lepidopilum latifolium* (Müll. Hal.) Mitt., J. Linn. Soc., Bot. 12: 380. 1869. Protologue. Insula Trinidad Antillarum, ubi monte Tocuche leg. *Crüger*.

Lepidopilum radicale Mitt., J. Linn. Soc., Bot. 12: 378. 1869. Protologue. [Ecuador] Andes Quitenses, Antombos ad saxa cataractae (5000 ped.), *Spruce, n. 765*; ad pedem montis Tunguragua (7000 ped.), *Spruce, n. 767*; fl. Bombonasa ad *Iriarteae ventricosae* radices (1300 ped.), *Spruce, n. 768, 769, 770*; Tunguragua, ad arborum radices, *Spruce, n. 771*. Type. Antombos, *Spruce, 765* (FH, syntype).

Lepidopilum filiferum Besch. *in* Fourn., Mexic. Pl. 1(Crypt.): 42. 1872. *Crossomitrium filiferum* (Besch.) Broth., Nat. Pflanzenfam. I(3): 957. 1907. Protologue. [Mexico] Cordova, ad cortices arborum (*Bourg*[*eau*] *n*^{o} *2137*, proparte, mart. 1866).

Lepidopilum falcatulum Müll. Hal., Linnaea 38: 648. 1874. Protologue. Mexico, Mirador, 4000′, ad truncos in sylvis: *C. Mohr* 1857.

Lepidopilum livens Besch., Bull. Herb. Boissier 2: 396. 1894. Protologue. An verwittertem Holz in feuchten, schattigen Wäldern am Vulkan Turialba. 2000 m. Costa-Rica. 17 Januar 1882 [*F. Lehmann*] *N*^{o} *1126*. Type. An verwittertem Holz in feuchten, schattigen Wäldern am Vulkan Turialba. 2000 m, 17.1.1882, Costa-Rica. 17 Januar 1882 [*F. C. Lehmann*] *1126*. (US, isotype), *syn. nov.*

Lepidopilum stolonaceum Müll. Hal., Hedwigia 37: 245. 1898. Protologue. Portorico, prope Manatí, Aprili 1887: *P. Sintenis* in Hb. Krug et Urban.

Lepidopilum dominicense E. B. Bartram, Bull. Brit. Mus. (Nat. Hist.), Bot. 2(2): 46. 1955. Protologue. [Dominica] Morne Micotrin, on trees, 945 m, [*W. R. Elliiot*] *1231a*. Type. Flora of Dominica. Locality: On trees, Morne Micotrin, 3100 ft. Date: 13.1.1896, Coll. *W. R. Elliot 1231a* (FH, isotype).

Plants small to medium-sized, 2–6 cm long, glossy, dark green, green, yellowish green, or reddish, in lax tufts. Primary stems prostrate and creeping. Secondary stems erect-ascending, or pendent, sparsely and irregularly branched, branches at times attenuate-foliate, hyaline to yellowish when young, becoming reddish with age, loosely or strongly complanate-foliate; stems in cross section with well-developed hyalodermis, 1–3 layers of small, thick-walled subepidermal cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong, hyaline; rhizoids on primary stems and at base of secondary stems, from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves distantly or closely spaced, weakly dimorphic, loosely or strongly flattened. Lateral leaves spreading, flat or sometimes crispate when dry, falcate-spreading when wet, oblong to oblong-lanceolate, 2–4 mm long, asymmetric, falcate to sigmoid, short-acute to short-acuminate; margins serrate to serrulate, at times subentire above, plane, often broadly infolded on one side at base, elimbate or obscurely bordered by a single row of elongate cells; costae double, slender, 1/4–1/3 the leaf length, diverging throughout, smooth at back, not projecting at the apices; cells smooth, upper cells narrowly or broadly linear-fusiform, 80–120 × 10–15 µm, thin-walled, not porose, becoming oblong-rectangular to oblong-fusiform below; alar cells not differentiated. Dorsal leaves erect to appressed, ovate to oblong-lanceolate, symmetric, 2–3 mm long. Asexual reproduction by deciduous leaves or fusiform, multicellular, uniseriate propagula from clusters of initials abaxial to the leaf insertions at base of costae. Autoicous or synoicous. Setae elongate, 4–10 mm long, red to reddish orange, papillose throughout. Capsules erect to suberect, oblong-cylindrical, 1–2 mm long, neck well developed; exothecial cells reddish, oblate in 3–4 rows at mouth, those below oblong to rounded-rectangular, thick-walled, not collenchymatous; stomata rudimentary, 2–4-celled, on neck; opercula high-conic, 1.0–1.5 mm long; annuli of 13–17 rows of thin-walled cells, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome very narrowly triangular, median furrow absent, dorsal (outer) surface broad, whitish yellow, densely papillose throughout, trabeculae thin, median lines faint, ventral (inner) surface narrow, 1/3 or less the width of the dorsal surface, red, lightly papillose, deposition thick; endostome as long or longer than the exostome, pale yellowish, papillose throughout, basal membranes high, segments broad, concave-keeled, not perforate, cilia absent. Spores rounded, 10–13 µm, smooth to lightly papillose. Calyptrae campanulate-mitrate, 1.0–1.8 mm long, reddish yellow, irregularly lobed at base, scabrous above, often with many multicellular ramenta.

Illustrations. Schwägrichen (1816, Pl. 82); Bartram (1949, Fig. 138 G & H, as *L. radicale*; Fig. 139 A–C, as *L. mohrianum*; Fig. 139 D–F, as *L. subenerve*); Welch (1966, Figs. 207–215, as *L. falcatulum*; Figs. 216–224, as *L. filiferum*; Figs. 225–233, as *L. mohrianum*; Figs. 257–267, as *L. radicale*; Figs. 268–274, as *L. scabrisetum*); Welch (1969, Figs. 199–207, as *L. stolonaceum*); Florschütz-de Waard (1986, Fig. 135; Fig. 136 as *L. stolonaceum*; Fig. 137, as *L. radicale*); Churchill (1988, Figs. 19 & 20); Sharp *et al.* (1994, Fig. 603, as *L. mohrianum*; Fig. 604; Fig. 607, as *L. falcatulum*; Fig. 610, as *L. piliferum*; Fig. 615, as *L. radicale*); Duarte Bello (1997, Pl. 233, as *L. stolonaceum*); Buck (2003, Fig. 96); Vaz and Costa (2006b, Figs. 61–70). Figure 200.

Habitat. On tree roots, trunks, branches, twigs, vines, lianas, leaf petioles, leaves, logs, rotting wood, rocks, boulders, and moist banks; sea level to 2550 m.

Distribution in Central America. BELIZE. Cayo: *Allen 18095* (MO); Toledo: *Allen 18970* (BRH, MO). GUATEMALA. Alta Verapaz: *Steyermark 44420* (F, FH, NY); El Progreso: *Sharp 2718a* (FH); Izabal: *Standley 72417* (F, FH); Quetzaltenango: *Crosby 2832* (MO, NY); Quiché: *Sharp 2410* (FH); San Marcos: *Crosby 2845* (MO, NY). EL SALVADOR. Santa Ana: *Watson ES-0091* (MO). HONDURAS. Atlántida: *Allen 17340* (MO); Comayagua: *Allen 13976* (MO); Lempira: *Allen 12043* (MO, NY, TEFH); Francisco Morazán: *Allen 12354* (MO, TEFH); Ocotepeque: *Allen 14434* (MO, TEFH); Olancho: *Allen 12417* (MO, NY, TEFH); Yoro: *Allen 13564* (MO). NICARAGUA. Jinotega: *Standley 10873* (F); Matagalpa: *Croat 43145* (MO); Rivas: *Granzow de la Cerda GC-1671* (DUKE). COSTA RICA. Alajuela: *Crosby & Crosby 5900* (MO); Cartago: *Crosby & Crosby 5907* (CR, MO); Guanacaste: *Dauphin 1909* (MO); Heredia: *Crosby & Crosby 6014* (CR, MO); Limón: *Steere CR-184* (NY); Puntarenas: *Lyon 148* (CR, MO); San José: *Crosby 9683* (MO). PANAMA. Bocas del Toro: *Allen 5571* (MO); Canal Area: *Steyermark & Allen 17165* (MO); Chiriquí: *Crosby 4011a* (MO, PMA); Coclé: *Crosby 4404* (MO, PMA); Colón: *Crosby 10327* (MO); Darién: *Allen 8870* (MO); Panamá: *Folsom & Maas 5206* (MO, NY, PMA, US); Veraguas: *Crosby 10239* (MO).

World range: Mexico; Central America; Caribbean; Western and Northern South America, Brazil.

Lepidopilum scabrisetum is a common, exceedingly variable species in Central America. It grows on nearly every type of substrate, but seems to be especially common as an epiphyte on twigs and leaves. It has closely or distantly spaced, usually dimorphic leaves: lateral leaves oblong to oblong-lanceolate, strongly flattened, asymmetric, falcate to sigmoid; dorsal leaves ovate to oblong-lanceolate, erect to appressed, symmetric. When dry the plants often have strongly complanate-foliate stems. The leaves have shortly acute to short-acuminate apices; serrate to serrulate upper margins that are elimbate or obscurely bordered; thin-walled, narrowly to broadly fusiform upper cells; and short costae that typically end just below midleaf. Asexual reproduction by deciduous leaves or uniseriate propagula clustered at the leaf bases is common in the species. *Lepidopilum scabrisetum* is synoicous or autoicous, and collections often have sporophytes. Its long setae are often spinose-papillose throughout. The calyptrae typically have many multicellular ramenta.

The incredible variability exhibited by *Lepidopilum scabrisetum* has been discussed in considerable detail by Churchill (1988) and Buck (1998). A striking form of the species with deciduous leaves has been called *L. stolonaceum*. This form has short-acute to apiculate leaves that are more broadly oblong than is typical for the species, and often its branches are naked due to the complete loss of their leaves. The name *L. radicale* is sometimes applied to plants with subentire upper leaf margins, and *L. latifolium* has been applied to robust plants with large, oblong to obovate leaves. In Central America *L. scabrisetum* will most likely be confused with those *Lepidopilum* species that have asymmetric, elimbate, and falcate lateral leaves: *L. brevipes*, *L. cuspidans*, and *L. muelleri*. Most collections of *L. brevipes* and *L. cuspidans* are more slender than *L. scabrisetum* and they usually have narrower leaves, but there are forms of *L. scabrisetum* that are gametophytically identical to these species. *Lepidopilum brevipes* and *L. cuspidans* differ from *L. scabrisetum* in having shorter setae (1.0–3.5 mm vs. 4–10 mm). In addition, *L. brevipes* has mostly naked calyptrae and can sometimes have long-acuminate leaves. *Lepidopilum muelleri* differs from *L. scabrisetum* in having somewhat longer (3–5 mm), long-acuminate leaves. As noted by Churchill (1988) the *latifolium*-form of *L. scabrisetum* can have leaves very similar to those of *L. pallidonitens*. In *L. pallidonitens*, however, the leaves are usually tightly flattened and always short-apiculate.

15. *Lepidopilum stillicidiorum* Mitt., J. Linn. Soc., Bot. 12: 373. 1869. Protologue. [Ecuador] Andes Quitenses, in sylva Canelos in stillicidiis (3000 ped.), *Spruce, n. 735*.

Lepidopilum carneum E. B. Bartram, Contr. U.S. Natl. Herb. 26: 103. 1928. Protologue. On tree, La Estrella, Province of Cartago, Costa Rica, *Paul C. Standley*, March 26 and 27, 1924, *no. 39202*. Types. Plants of Costa Rica. On tree. La Estrella, Province of Cartago, March 26, 27, 1924, *No. 39202, Paul C. Standley*, Collector (US, holotype; FH, isotype).

Plants medium-sized to robust, 4–9 cm long, green, dark green, or yellowish brown, in lax or dense tufts. Stems prostrate and creeping, irregularly and sparsely branched, hyaline to yellowish when young, becoming darker with age; stems in cross section with a moderate-sized 1–3-stratose hyalodermis, 1–2 layers of smaller, thick-walled subepidermal cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong, hyaline; rhizoids on stems when in contact with substrate, from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves crowded to somewhat distant, crispate when dry. Lateral leaves wide-spreading, oblong-lanceolate or oblong-lingulate, 3.5–5.0 mm long, asymmetric, obtuse or rounded, apiculate or short-acuminate; margins serrulate to serrate above, entire below, limbate, by 2–4 rows of elongate cells, plane above, usually broadly infolded on one side at base; costae double, thin, ending 2/3–3/4 the leaf length, diverging throughout, in lateral leaves one fork often approaching the margins, smooth at back, not projecting at the apices; cells smooth, median cells broadly hexagonal, 100–50 × 44–15 µm, thin-walled, lower cells oblong to rectangular; alar cells not differentiated. Dorsal leaves erect when wet, ovate to ovate-lanceolate, 3–4 mm long, symmetric, short-acuminate, margins serrulate to serrate above, entire below, limbate, by 2–4 rows of elongate cells, plane. Asexual propagula fusiform, multicellular, uniseriate, arising from clusters of initials abaxial to the leaf insertions at base of costae. Dioicous. Sporophytes not known from Central America or seen, description from Churchill (1988). Setae short, 3.5 mm long, papillose throughout. Capsules 1.0 mm long. Calyptrae mitrate, 1.5 mm long, short-campanulate, hairy.

Illustrations. Welch (1966, Figs. 176–185); Churchill (1988, Fig. 42); Sharp *et al.* (1994, Fig. 606); Churchill and Linares (1995, Fig. 42 a–d). Figure 201.

Habitat. On rocks along streams, terrestrial on moist soil banks or humus, and tree branches; 620–1840 m.

Distribution in Central America. COSTA RICA. Cartago: *Crosby & Crosby 5816* (CR, MO); Heredia: *Crosby & Crosby 6069* (CR, MO); San José: *Crosby & Crosby 5968* (MO). PANAMA. Chiriquí: *Antonio 4885* (MO, NY, PMA); Veraguas: *Crosby 10193* (MO).

World range: Mexico, Central America; Western South America.

Lepidopilum stillicidiorum is a medium-sized to robust species with leaves that are typically strongly contorted when dry. The species sometimes occurs on rocks in or along streams, but it can also be terrestrial or found on tree branches. It has prostrate or creeping stems that are irregularly branched and have a variably developed, 1–3-stratose hyalodermis. The leaves of *L. stillicidiorum* are strongly dimorphic with asymmetric, oblong-lanceolate or oblong-lingulate lateral leaves and ovate to ovate-lanceolate dorsal leaves. The leaves have obtuse to rounded, usually apiculate apices and consistently bordered margins. The leaf border varies considerably depending on its position: weakly or not developed at base, strongly developed (to 5 cells wide) at midleaf, and weakly developed (2 cells wide) above. The leaf borders are not confluent at the apex. *Lepidopilum stillicidiorum* leaves have lax, broadly hexagonal upper cells and thin, smooth costae that end well above midleaf and do not project at the tips. Often one fork of the costae ends near or on the leaf border. *Lepidopilum stillicidiorum* is dioicous, and only male plants are known from Central America. Its sporophytes are extremely rare, and the only description of them indicates merely that the setae are short (3.5 mm long) and papillose throughout.

The presence of strongly contorted, oblong-lanceolate or oblong-lingulate lateral leaves with rounded to obtuse, apiculate to shortly acuminate apices separates *Lepidopilum stillicidiorum* from most other Central American species of *Lepidopilum*. Indeed, the only other Central American spe-

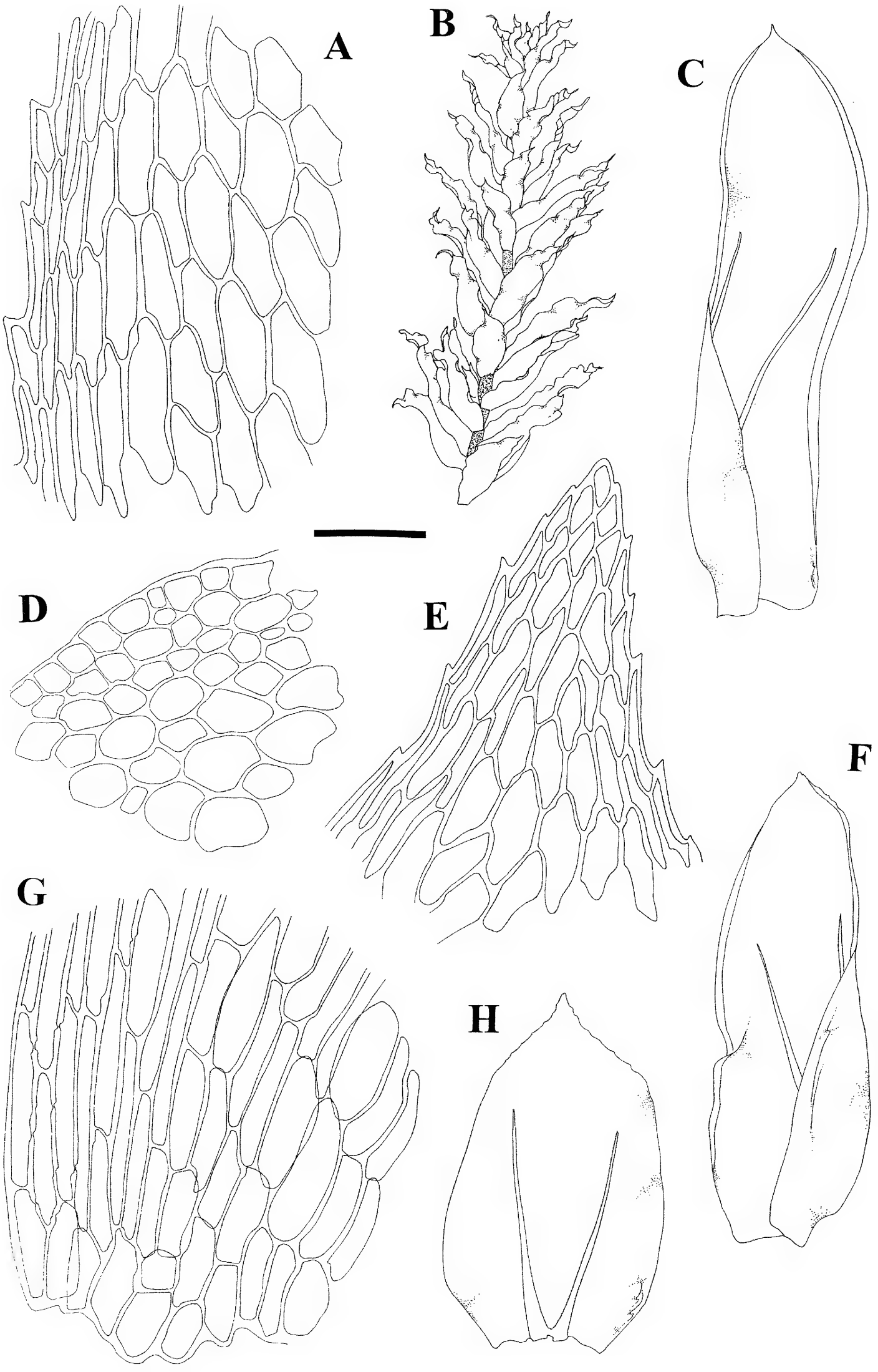
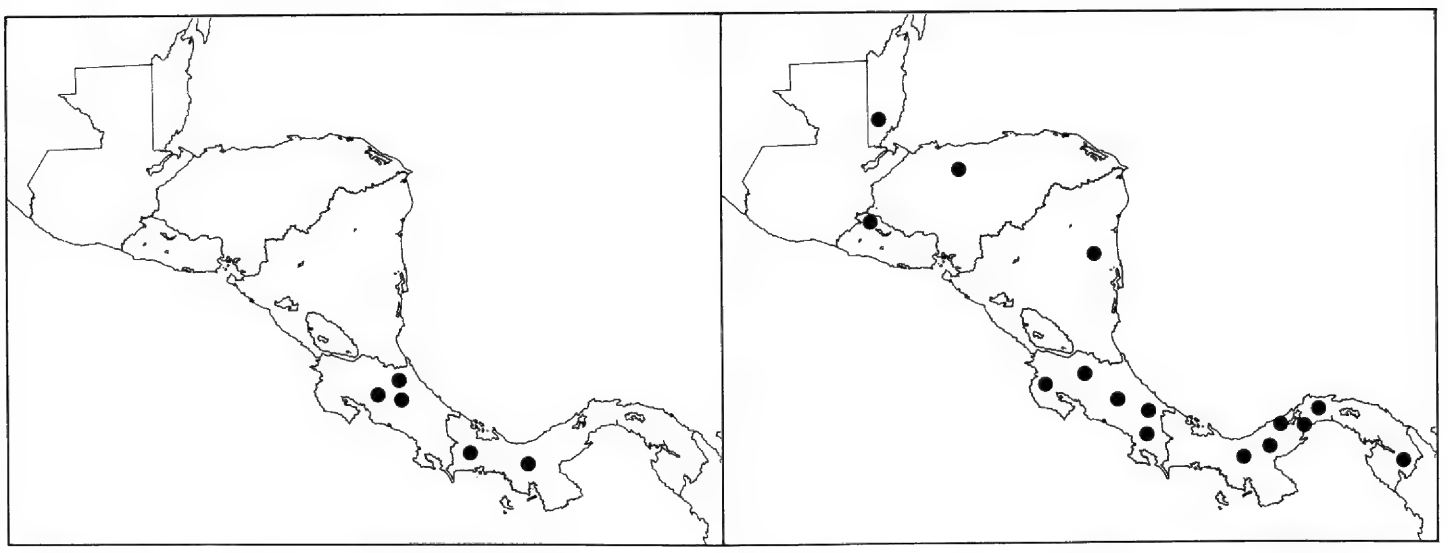


Figure 201. *Lepidopilum stillicidiorum*. A. Median leaf cells and margin. B. Habit. C & F. Lateral leaves. D. Stem in cross section. E. Leaf apex. G. Basal and alar cells. H. Dorsal leaf. Scale in mm: bar = 0.08 (D); bar = 0.09 (A, E, G); bar = 0.9 (C, F, H); bar = 3.2 (B). A, E, G from *Churchill 14050*; B from *Antonio 4885*; all other figure parts from *Standley 39202*.



Lepidopilum stillicidiorum *Lepidopilum surinamense*

cies of *Lepidopilum* with such strongly contorted leaves are *L. polytrichoides*, *L. permarginatum*, and *L. tortifolium*. *Lepidopilum polytrichoides* differs from *L. stillicidiorum* in having sharply serrate to spinose, long-acuminate lateral leaves that are often over 6 mm long. Although both species have short setae, *L. polytrichoides* is synoicous and sporophytes are often encountered. *Lepidopilum permarginatum* differs from *L. stillicidiorum* in having short- to long-acuminate leaves with very strong leaf borders that are typically confluent at the apex. *Lepidopilum tortifolium* is similar to *L. stillicidiorum* in having broadly rounded, apiculate leaves, but differs in having shorter (2–3 mm vs. 4–5 mm) obovate, ovate-oblong, or oblong lateral leaves. The leaves of *L. stillicidiorum* often taper and become progressively smaller toward the apex, and for that reason care should be taken when measuring its lateral leaves; only the largest leaves at the base of stems should be measured.

16. *Lepidopilum surinamense* Müll. Hal., Linnaea 21: 193. 1848. *Hookeria surinamensis* (Müll. Hal.) Müll. Hal., Syn. Musc. Frond. 2: 207. 1851. Protologue. [Suriname] An Baumstämmen in den Urwäldern bei *Mariepaston*. Mai 1846 steril. Hb. *Kegel. No. 1406*.

Lepidopilum contiguum Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32(1): 193. 1894. Protologue. [Costa Rica] Forêts du Rio Naranjo (*Pitt*[*ier*] *n*^{o} *5657*). Type. Costarica: forêts du Rio Naranjo. Leg. *Tonduz*, 1893. H. Pittier & Th. Durand, Plantae Costaricenses Exsiccatae *No. 5657* (NY, isotypes), *syn. nov.*

Lepidopilum steyermarkii E. B. Bartram, Fieldiana, Bot. 28: 6. 1951. Protologue. [Venezuela] Collected between Hacienda Agua Blanca above La Azulita and Río Capaz, state of Mérida, alt. 975 m, April 26, 1944, *Julian A. Steyermark 56138*. Type. Plants of Venezuela. State of Mérida: between Hacienda Agua Blanca above La Azulita and Río Capaz, altitude 975 meters. *Julian A. Steyermark 56138*, April 26, 1944 (FH, isotype), *syn. nov.*

Plants medium-sized, 1–4.5 cm long, glossy, light to dark green or reddish yellow, in loose tufts. Primary stems prostrate and creeping. Secondary stems ascending to erect, not or sparsely branched, hyaline to yellowish when young, becoming red to red brown with age; stems in cross section with a hyalodermis, 3–5 layers of small, thick-walled subepidermal cells, cortical cells enlarged, firm- to thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong, hyaline; rhizoids on primary stems and secondary stems, at times densely tomentose, from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, often pinnately or bipinnately branched. Leaves closely or somewhat distantly spaced, weakly to not dimorphic, erect-spreading to spreading when wet, erect and somewhat contorted when dry, ovate-oblong, oblong, or obovate, 1.8–3.0 mm long, symmetric or asymmetric, short-acute to rounded-apiculate, apices often twisted; margins sharply serrate above, serrulate or subentire below, elimbate or weakly limbate by 1–2 rows of elongate cells, plane or broadly incurved on one side below; costae double, 1/3–2/3 the leaf length, diverging throughout, smooth at back, not projecting at the apices; cells smooth, median cells rhomboidal, fusiform, or oblong-hexagonal, 38–72 × 10–22 μm, thick-walled, sometimes porose, lower cells

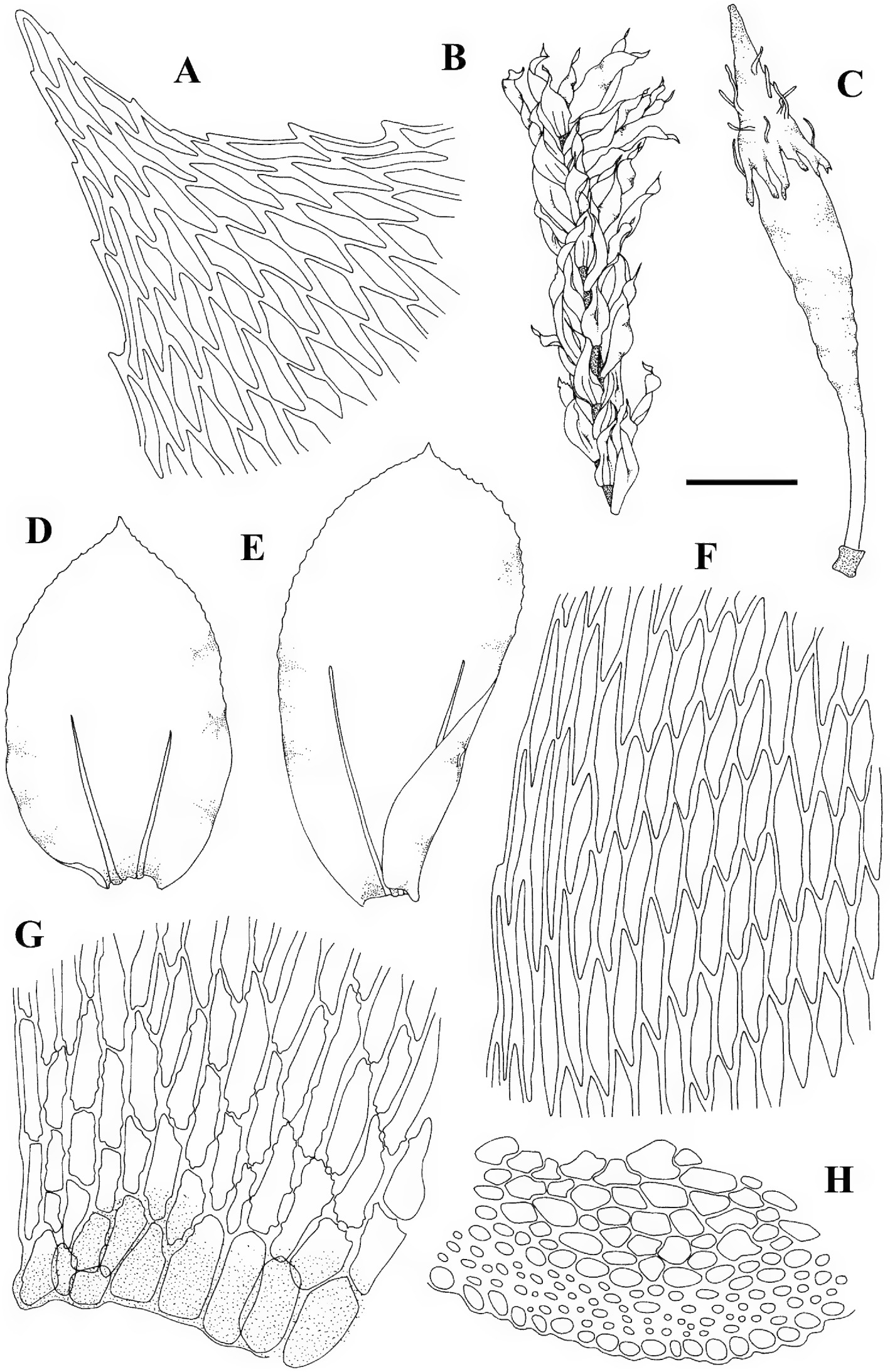


Figure 202. *Lepidopilum surinamense*. A. Leaf apex. B. Habit. C. Seta, capsule, and calyptra. D. Dorsal leaf. E. Lateral leaf. F. Median cells and margin. G. Basal and alar cells. H. Stem in cross section. Scale in mm: bar = 0.06 (A, F, G); bar = 0.09 (H); bar = 0.6 (D, E); bar = 1.0 (B); bar = 1.96 (C). A, C, G from *Allen 18712*; B from *Crosby 3950*; all other figure parts from *Allen 25536*.

elongate-fusiform, firm-walled, often porose, cells across the base enlarged, subrectangular, yellow to reddish yellow; alar cells not differentiated. Asexual propagula fusiform, multicellular, uniseriate, from clusters of initials abaxial to the leaf insertions at base of costae, occasionally in dense clusters at ends of secondary stems and branches. Dioicous. Setae short and thick, 1.0–2.5 mm long, red to reddish orange, smooth below, papillose above, or smooth throughout. Capsules erect, ovoid- to oblong-cylindrical, 1.5–2.5 mm long, neck well developed, papillose-roughened; exothecial cells quadrate in 2–3 rows at mouth, those below oblong to rectangular, with thick vertical walls and thin horizontal walls; stomata rudimentary, 3–5-celled, on neck; opercula high-conic, 1.0 mm long; annuli of 8–10 rows of thin-walled, quadrate to oblate cells, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome very narrowly triangular, yellowish white, median furrow absent, dorsal (outer) surface lightly papillose throughout, trabeculae moderately thickened, median lines faint, ventral (inner) surface as wide as the dorsal surface, yellow, lightly papillose, deposition thin; endostome as long as the exostome, pale yellowish, papillose throughout, basal membranes medium high, segments broad, weakly concave-keeled, not perforate, cilia absent or rudimentary. Spores rounded, 12–18 μm, smooth to lightly papillose. Calyptrae campanulate-mitrate, 1–2 mm long, reddish yellow, irregularly lobed at base, scabrous, with many multicellular ramenta.

Illustrations. Welch (1974, Figs. 304–316, as *L. biductulosum*); Churchill (1988, Fig. 49); Florschütz-de Waard (1986, Fig. 131); Churchill (1994, Fig. 12 C & D); Buck (2003, Fig. 97); Vaz and Costa (2006b, Figs. 81–87). Figure 202.

Habitat. On trees, branches, twigs, lianas, roots, rocks, fallen branches, and rotting logs; sea level to 1000 m.

Distribution in Central America. BELIZE. Toledo: *Allen 18712* (BRH, MO). EL SALVADOR. Chalatenango: *Kovar 16* (NY). HONDURAS. Yoro: *Allen 13481* (MO). NICARAGUA. Zelaya: *Stevens 4892* (MO). COSTA RICA. Alajuela: *Standley 40142b* (FH); Cartago: *Standley 33611f* (FH); Guanacaste: *Alfaro* (FH); Limón: *Stevens 23718* (MO); Puntarenas: *Liesner 1704C* (MO). PANAMA. Canal Area: *Crosby 3950* (MO, NY, PMA); Coclé: *Crosby 4390* (FH, MO, NY, PMA, US); Colón: *Crosby 10795* (MO); Darién: *Allen 8822A* (MO); Panamá: *Crosby 4344* (MO); Veraguas: *Crosby 10139* (MO).

World range: Central America; Western, Northern, and Southern South America, Brazil.

Lepidopilum surinamense is a medium-sized species with glossy, often reddish yellow plants. Although it occurs in Central America on a variety of habitats, the species most often grows on twigs or small branches, and it has erect secondary stems. The stems of *L. surinamense* are evenly foliate with leaves that are erect, somewhat contorted when dry, and erect-spreading on all sides when wet. The leaves are weakly dimorphic: ovate-oblong or oblong lateral leaves with one margin often broadly incurved below; obovate dorsal leaves with plane margins. Its leaves have sharply serrate upper margins that are variously bordered by 1–2 rows of elongate cells; fairly strong, moderately long (1/3–2/3 the leaf length) costae that do not project at the tips; rhomboidal to fusiform, relatively broad, thick-walled, often porose upper cells; elongate-fusiform basal cells; and apices that are often twisted whether wet or dry. As noted by Florschütz-de Waard (1986), at times the leaves are "irreversibly shriveled after drying," and these leaves are very different in shape and areolation from typical leaves. Plants of *L. surinamense* have asexual propagula that are typically found abaxial to the leaf insertions at the base of the costae, but occasionally (*e.g.*, *Stevens 4895B*, MO, Nicaragua; *Steere CR-185*, NY, Costa Rica) the stems and branches have dense, terminal clusters of gemmae.

The setae in *L. surinamense* are short (1.0–2.5 mm), stout, and either lightly papillose above or smooth throughout. The ovoid- to oblong-cylindrical capsules have oblong to rectangular exothecial cells with very thick vertical walls but thin horizontal walls. Although *L. surinamense* has a daltoniceous peristome, unlike in other members of the genus the exostome teeth on the ventral (inner) surface are not secondarily thickened and colored in a narrow median band running the length of the teeth.

In Central America *L. surinamense* has often been confused with *L. amplirete* or *L. polytrichoides*. All three species have similarly shaped leaves with fusiform upper cells. The sporophytes of *L. amplirete* differ from those of *L. surinamense* in having longer (5–13 mm vs. 2.5–3.0 mm) setae,

somewhat shorter capsules (1.5–2.0 mm vs. 1.5–3.0 mm), and strongly collenchymatous exothecial cells. However, their gametophytes are very similar and collections without sporophytes can be very difficult to place. At times *L. amplirete* has somewhat flattened, widely spaced leaves, and this form of the species differs considerably from *L. surinamense*, which usually has closely spaced, evenly foliate leaves. There are, though, collections of *L. amplirete* and *L. surinamense* with plants that are identical in aspect. *Lepidopilum surinamense*, however, nearly always has thick masses of rhizoids on its primary stems. These rhizoids are densely, at times pinnately or bipinnately, branched. In contrast, the primary stems of *L. amplirete* have sparsely and irregularly branched rhizoids. Plants of *L. polytrichoides* can be similar in size to *L. surinamense*, and both species have weakly bordered leaves, comparable upper leaf cells, and short setae. *Lepidopilum polytrichoides* differs from *L. surinamense* in having longer (3–8 mm), short- to long-acuminate leaves, more strongly papillose setae, and a synoicous sexual condition.

The name *Lepidopilum flexifolium* has often been applied to *L. surinamense*. That name, however, is illegitimate because its protologue included the type of an earlier name (*L. biductulosum* (P. Beauv.) Wijk & Margad.). *Lepidopilum biductulosum* is a synonym of *L. polytrichoides*. Florschütz-de Waard (1986) and Churchill (1988) considered *L. rotundifolium* a robust expression of *L. surinamense*, but that taxon is treated here as a synonym of *L. curvifolium*.

17. *Lepidopilum tortifolium* Mitt., J. Linn. Soc., Bot. 12: 374. 1869. Protologue. [Colombia] Andes Bogotenses, prope Bucaramanga ad lapides rivuli (5000 ped.), *Weir, n.* 147. [Ecuador] Andes Quitenses, fl. Bombonasa (1200 ped.), *Spruce, n. 783*. Types. Ecuador. Bombonasa, *Spruce 783* (NY, lectotype [see Buck 1987]; FH, isolectotype).

Hookeria riparia Mitt., J. Linn. Soc., Bot. 12: 345. 1869. Protologue. [Ecuador] Andes Quitenses, in ripis fl. Bombonasa (1200 ped.), *Spruce, n. 593*. Type. Andes Quitenses, in ripis fl. Bombonasa, terrestris 1200 ped., *Spruce 593* (NY, holotype).

Lepidopilum crispifolium E. B. Bartram, Rev. Bryol. Lichénol. 33: 11. 1964. Protologue. [Ecuador] On rocks and tree bases, Shinguipino rain forest between Rio Napo and Tena, 8 km S.E. of Tena, c. 1500 ft., [*Grubb, Lloyd, Pennington & Whitmore*] *2939, 2942a, 2947* type. Type. Ecuador. On outcropping rock in forest floor. Singuipuri [sic] rain forest between Rio Napo and Tena. 8 km S.E. of Tena. c. 1500 ft. 29.8.1960, *P. J. Grubb 2947* (FH, holotype), *syn nov*.

Plants small, medium-sized, or robust, 2–8 cm long, green, dark green, or yellowish brown, in lax or dense tufts. Stems prostrate and creeping, irregularly and sparsely branched, hyaline to yellowish when young, becoming darker with age; stems in cross section with a moderate-sized hyalodermis, 1–2 layers of small, thick-walled subepidermal cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong, hyaline; rhizoids on stems when in contact with substrate, from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves crowded to somewhat distant, crispate to tortuose when dry. Lateral leaves wide-spreading, obovate, ovate-oblong, or oblong, 2–3 mm long, asymmetric or symmetric, obtuse or rounded, apiculate or short-acuminate; margins serrulate to serrate above, entire below, limbate, by 2–5 rows of elongate cells, plane above, at times broadly infolded on one side at base; costae double, thin, ending 1/3–2/3 the leaf length, diverging throughout, one fork often approaching the margins, smooth at back, not projecting at the apices; cells smooth, median cells broadly hexagonal to rhomboidal, 40–60 × 25–35 µm, thin-walled, lower cells rectangular; alar cells not differentiated. Dorsal leaves erect when wet, ovate, oblong-ovate, or suborbicular, 2 mm long, symmetric, short-acuminate; margins serrulate to serrate above, entire below, limbate, by 2–5 rows of elongate cells, plane. Asexual propagula not seen. Dioicous. Setae elongate, 10–12 mm long, red to reddish orange, densely papillose throughout. Capsules erect, ovoid to oblong-cylindrical, 1.0–1.5 mm long, neck weakly developed; exothecial cells reddish, oblate in 4–6 rows at mouth, those below long-rectangular, evenly firm- to thick-walled, not collenchymatous; stomata rudimentary, 3–6-celled, on neck; opercula high-conic, 0.7–1.0 mm long; annuli of 7–12 rows of thin-walled cells, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome very narrowly triangular, median furrow absent, dorsal (outer) surface broad, whitish yellow, lightly papillose throughout, trabeculae thin, median lines faint, ventral (inner) surface narrow,

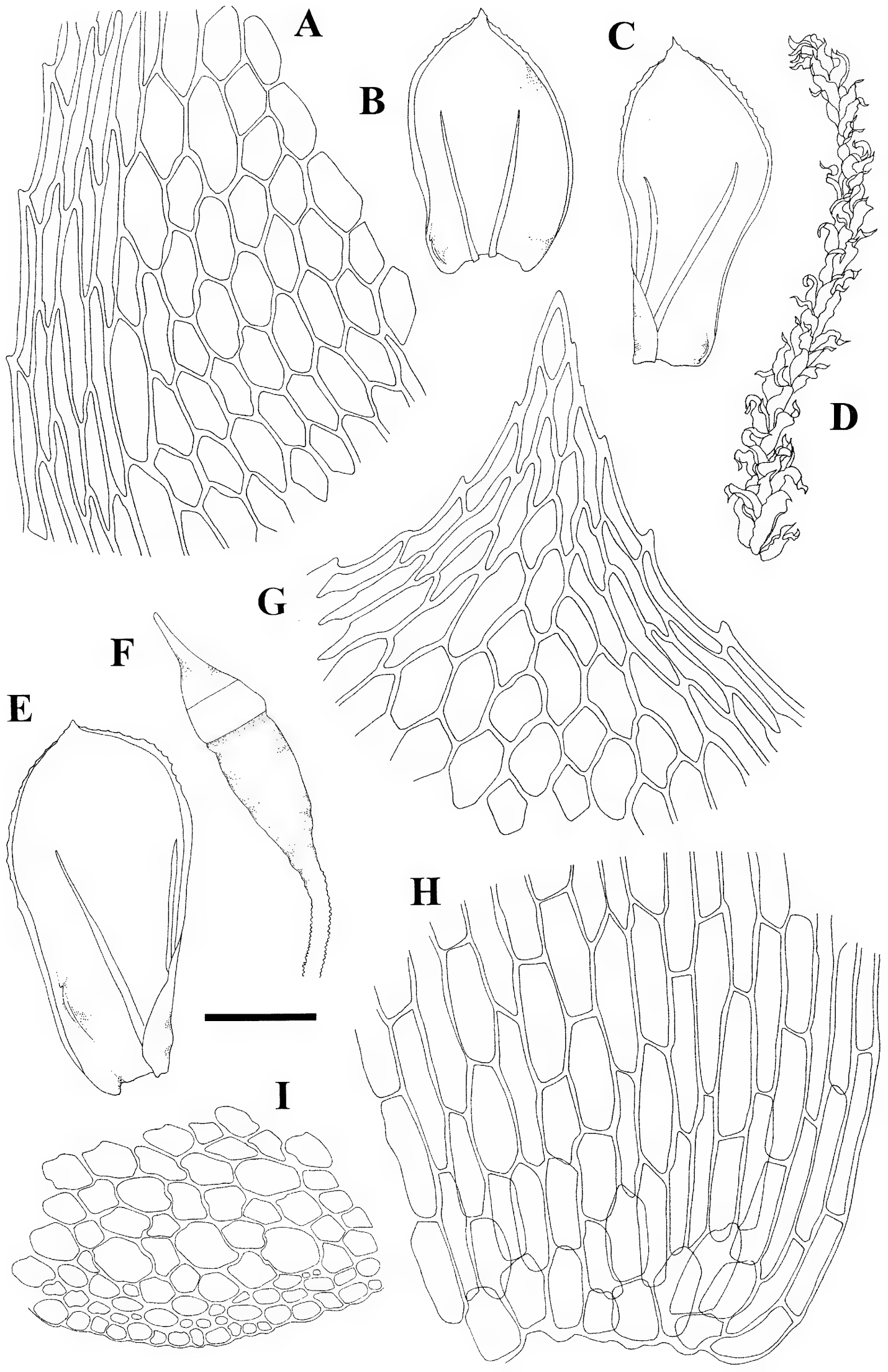
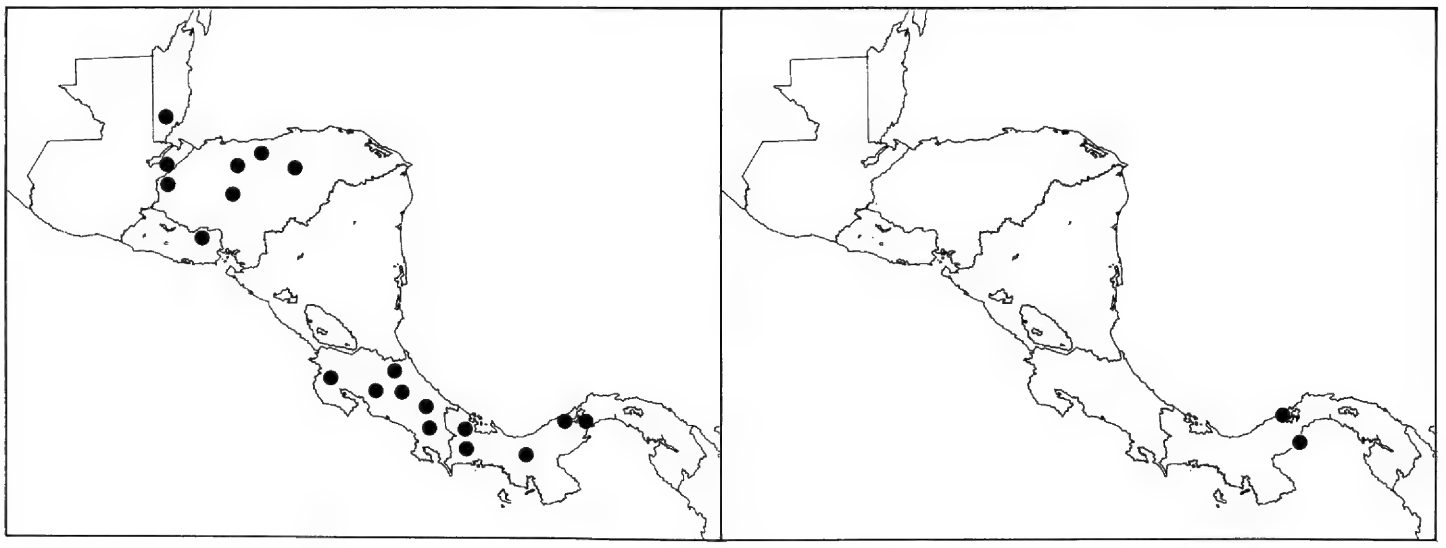


Figure 203. *Lepidopilum tortifolium*. A. Median leaf cells and margin. B. Dorsal leaf. C & E. Lateral leaves. D. Habit. F. Seta, capsule, annulus, and operculum. G. Leaf apex. H. Basal and alar cells. I. Stem in cross section. Scale in mm: bar = 0.06 (A, G, H); bar = 0.13 (I); bar = 0.6 (B, C, E); bar = 1.3 (F); bar = 1.96 (D). A, G, H from *Allen 5600*; all other figure parts from *Allen 5575*.



Lepidopilum tortifolium *Lepidopilum ultramarginatum*

1/3 or less the width of the dorsal surface, dark red, lightly papillose, deposition thick; endostome as long as the exostome, pale yellowish, densely papillose throughout, basal membranes high, segments broad, concave-keeled, not perforate, cilia absent. Spores rounded, 12–14 µm, smooth to lightly papillose. Calyptrae campanulate-mitrate, 2 mm long, whitish yellow, irregularly lobed at base, scabrous, usually with few to many multicellular ramenta.

Illustrations. Bartram (1949, Fig. 140 E–H); Welch (1966, Figs. 275–284); Churchill (1988, Fig. 44); Churchill (1994, Fig. 12 E & F); Sharp *et al.* (1994, Fig. 602); Buck (1998, Pl. 13 1–7); Buck (2003, Fig. 98). Figure 203.

Habitat. On wet ground and rocks along or in streams and springs, occasionally on rotting logs, branches, tree trunks, or stones in forest; 40–1800 m.

Distribution in Central America. BELIZE. Toledo: *Allen 18896* (BRH, MO). GUATEMALA. Izabal: *Steyermark 41866* (F, FH). EL SALVADOR. Morazán: *Carballo et al. 1122* (MO). HONDURAS. Atlántida: *Allen 17156* (MO); Comayagua: *Allen 11748* (MO, TEFH); Copán: *Allen 17747* (MO); Olancho: *Allen 12803* (MO); Yoro: *Allen 13578* (MO, TEFH). COSTA RICA. Cartago: *Maas 797* (MO); Guanacaste: *Gentry & Burger 2916* (MO); Heredia: *Hammel 7962* (MO); Limón: *Alfaro 107a* (FH); Puntarenas: *Hammel & Trainer 13982* (CR, MO); San José: *Stiles & Martin 2* (US). PANAMA. Bocas del Toro: *Allen 5575* (MO); Canal Area: *Nee 6610* (MO, PMA); Chiriquí: *McPherson 6825A* (MO); Colón: *Crosby 10469* (MO, PMA); Veraguas: *Crosby 10278* (MO).

World range: Mexico; Central America; Caribbean; Western and Northern South America, Brazil.

Although *Lepidopilum tortifolium* is variable in size, its plants are usually medium-sized, dark green, and when dry have strongly contorted leaves. The species is very often found on rocks in or along streams. It has prostrate or creeping stems that are irregularly branched and have a weakly developed hyalodermis. Its leaves are somewhat dimorphic, with usually asymmetric, obovate, ovate-oblong, or oblong lateral leaves and ovate, oblong-ovate, or suborbicular dorsal leaves. The leaves have obtuse to rounded, usually apiculate apices; lax, broadly hexagonal to rhomboidal upper cells; thin, smooth costae that end above midleaf and do not project at the tips; and consistently bordered margins. The strength of the leaf border varies considerably depending on its position: weakly or not developed at base, strongly developed (to five cells wide) at midleaf, and weakly developed (2 cells wide) above. The leaf border is not or barely confluent at the apex. At times one fork of the costae ends near or on the leaf border. *Lepidopilum tortifolium* is dioicous; its setae are long (over 10 mm) and densely papillose throughout.

Lepidopilum tortifolium can often be recognized by its occurrence on wet or submerged rocks and its dark green, strongly contorted leaves. In Central America the only other *Lepidopilum* species with strongly contorted leaves are *L. polytrichoides*, *L. permarginatum*, *L. inflexum*, and *L. stillicidiorum*. *Lepidopilum polytrichoides* is a much larger plant than *L. tortifolium*, with long-acuminate lateral leaves that are typically over 5 mm long and have sharply serrate to spinose margins. Also, it is

a synoicous species, with short setae (2–4 mm), and it often grows on twigs or tree trunks. *Lepidopilum permarginatum* and *L. inflexum* differ from *L. tortifolium* in having short- to long-acuminate leaves with very strong leaf borders that are typically confluent at the apex. *Lepidopilum stillicidiorum* is similar to *L. tortifolium* in having broadly rounded, apiculate leaves but differs in having longer (4–5 mm vs. 2–3 mm) leaves. *Lepidopilum tortifolium* is often confused with *Cyclodictyon subtortifolium*, because both are often aquatic species with leaves that are strongly contorted when dry. *Cyclodictyon subtortifolium* is a smaller plant than *L. tortifolium*, and its oblong to oblong-ovate lateral leaves are weakly asymmetric and have very broad marginal borders that are confluent at the apex. Furthermore, the costae of *C. subtortifolium* are longer (2/3–7/8 the leaf length) than those of *L. tortifolium*; they occasionally project at the apex; and they are often confluent with the leaf border on one side. In addition, the upper leaf cells of *C. subtortifolium* are considerably smaller (8–28 × 12–20 µm vs. 40–60 × 25–35 µm) than those of *L. tortifolium*.

18. *Lepidopilum ultramarginatum* B. H. Allen, *sp. nov.* Type. Panama. Colón: Beyond bench mark ("USA, BM, 2400 ft. ±"), 2 hours walk in from end of Santa Rita Road, which terminates 17.1 km after leaving Boyd–Roosevelt Highway, 09°15′N, 079°40′W, *Marshall R. Crosby 10466* (MO, holotype; PMA, isotype).

Species haec a *L. inflexo* foliis latioribus limbatis et setis longioribus differt.

Plants slender, 1–2 cm long, yellowish green to reddish yellow, in dense tufts. Primary stems prostrate and creeping. Secondary stems erect-ascending, sparsely branched, hyaline to yellowish when young, becoming reddish with age, somewhat complanate-foliate; stems in cross section lacking a hyalodermis, 1–3 layers of small, thick-walled sclerodermis cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong, hyaline; rhizoids usually on primary stems and at base of secondary stems, from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves distantly spaced, dimorphic, erect, flexuose-contorted when dry, erect-spreading, somewhat flattened when wet. Lateral leaves ovate-oblong to obovate, 2.0–2.5 mm long, asymmetric, abruptly short- to long-acuminate; margins sharply serrate to serrulate above, plane above, often broadly infolded on one side at base, strongly limbate, border at base consisting of 7–14 rows of elongate cells, border near apex of 4–8 rows of elongate cells; costae double, slender, 2/3–3/4 the leaf length, strongly diverging throughout, smooth at back, not projecting at the apices, one fork nearly always fused to the leaf border, occasionally both forks merged with margins; cells smooth, upper cells hexagonal to rhomboidal, 22–40 × 16–20 µm, firm-walled, porose, becoming fusiform to elongate-rhomboidal below, elongate-rectangular at base, sometimes porose; alar cells not differentiated. Dorsal leaves obovate, 2 mm long, symmetric; margins plane throughout; otherwise similar to lateral leaves. Asexual propagula not seen. Dioicous. Setae elongate, 10–12 mm long, red to reddish orange, spinose throughout. Capsules erect, ovoid to oblong-cylindrical, 1.0 mm long, neck well developed; exothecial cells reddish, oblate in 2–3 rows at mouth, those below subrectangular, firm-walled, not collenchymatous; stomata rudimentary, 3–6-celled, on neck; operculum and annulus not seen; peristome diplolepideous, exostome narrowly triangular, median furrow absent, dorsal (outer) surface broad, whitish yellow, lightly papillose throughout, trabeculae thin, median lines faint, ventral (inner) surface narrow, 1/3 or less the width of the dorsal surface, yellowish, lightly papillose, deposition thick; endostome as long as the exostome, pale yellowish, papillose throughout, basal membranes high, segments broad, concave-keeled, not perforate, cilia absent. Spores rounded, 12–14 µm, smooth to lightly papillose. Calyptra not seen.

Illustration. Figure 204.

Habitat. On tree trunks; 350–700 m.

Distribution in Central America. PANAMA. Colón: *Crosby 10310* (MO, NY, PMA); Panamá: *Crosby 4522* (MO, NY, PMA).

World range: Central America.

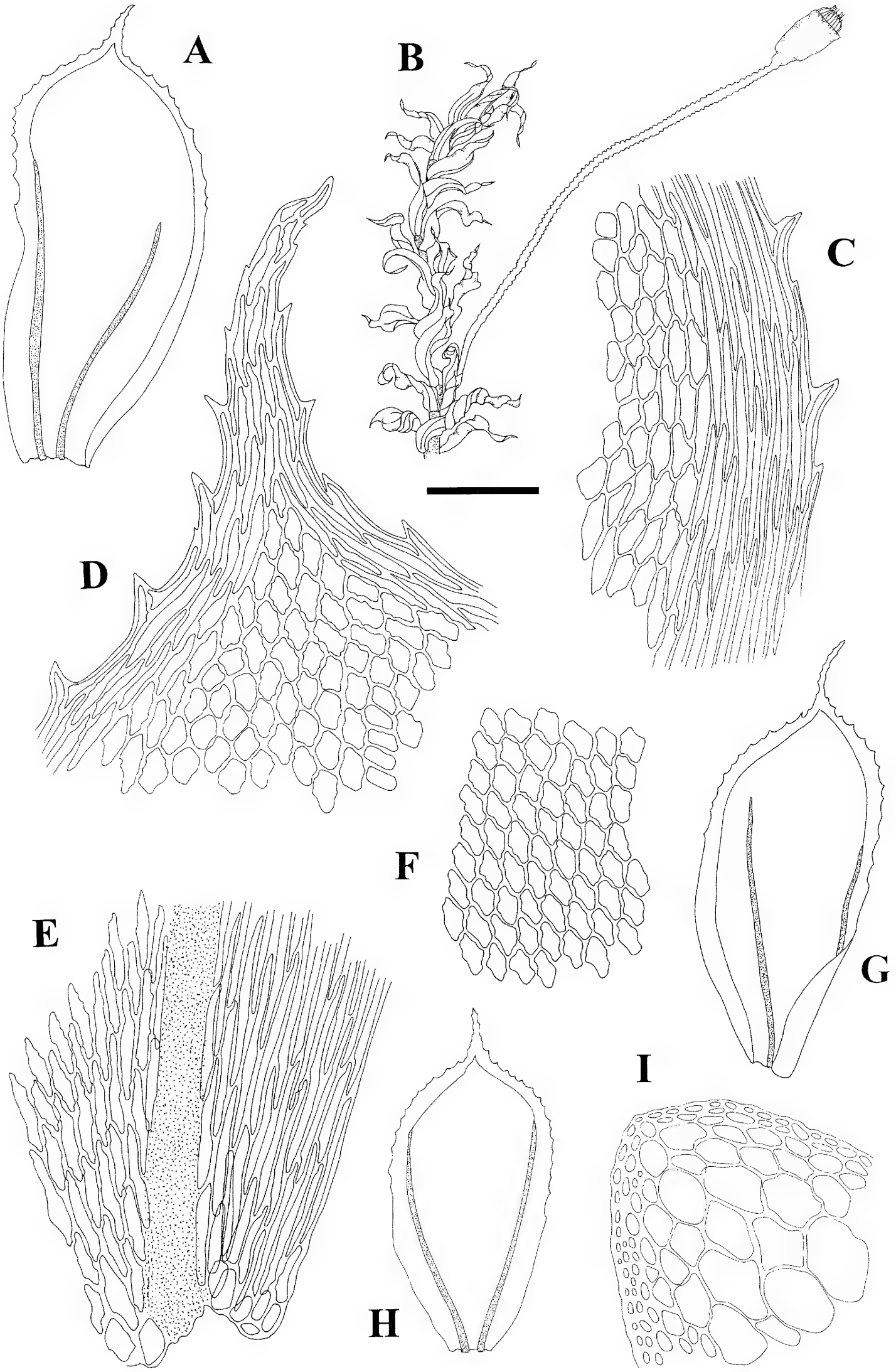


Figure 204. *Lepidopilum ultramarginatum*. A, G & H. Leaves. B. Habit. C. Upper leaf cells and margin. D. Leaf apex. E. Basal and alar cells. F. Median leaf cells between the costae. I. Stem in cross section. Scale in mm: bar = 0.08 (I); bar = 0.09 (C–F); bar = 0.6 (A, G, H); bar = 2.5 (B). All figure parts from *Crosby 10466* (type).

Lepidopilum ultramarginatum is a small, slender species with distantly spaced leaves. When dry the plants have erect, somewhat contorted-twisted leaves, but when wet they are erect to erect-spreading and somewhat complanate-flattened. It is the only species of *Lepidopilum* in Central America that lacks a stem hyalodermis. The stems have dimorphic leaves: large, asymmetric, ovate-oblong to obovate lateral leaves with one broadly infolded margin; small, symmetric, obovate dorsal leaves with plane margins. Its leaf margins, especially at base, are strongly bordered. Although the width of the border varies considerably from leaf to leaf, it often consists of 10–14 rows of linear cells at the leaf base. The leaves have sharply serrate to serrulate upper margins; firm-walled, porose, and hexagonal to rhomboidal upper cells; and strongly divergent costae with one and sometimes both forks merging nearly the entire length with the leaf border. The sporophytes of *L. ultramarginatum* have long setae (10–12 mm long) that are spinose throughout.

Lepidopilum exiguum is similar to *L. ultramarginatum* in having slender plants with distantly spaced, bordered, ovate-oblong to obovate leaves. That species, however, has leaves bordered by only 2–4 rows of elongate cells and short (2–3 mm long), papillose setae. In addition, the costae of *L. exiguum* do not or rarely merge with the leaf border. *Lepidopilum inflexum* is somewhat similar to *L. ultramarginatum* in size, and both species have strong leaf borders. In *L. inflexum*, however, the leaves are often contorted-twisted when wet, the leaf border consists of 2–4 rows of elongate cells, and the costae, which are nearly always free from the border, often end in single-celled spines. In addition, *L. inflexum* has short (3–5 mm) setae.

12. *Philophyllum* Müll. Hal., Bull. Herb. Boissier 6: 123. 1898.

Plants medium-sized, glossy, pale green, yellowish green, or reddish brown, in loose mats. Stems prostrate, simple or irregularly branched, complanate-foliate; young stems in cross section with outer cells smaller than the inner cells, otherwise cells thin-walled and undifferentiated, old stems in cross section with epidermis of 1–2 rows of small, thick-walled cells, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2 cells long, basal cell short-rectangular, reddish brown, upper cell elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, not or sparsely and irregularly branched. Leaves flattened, lateral leaves spreading, dorsal and ventral leaves erect to erect-spreading, laxly crispate when dry, flaccid when wet, somewhat distantly spaced, ovate-lanceolate, asymmetric, gradually narrowed to long or piliferous, flexuose or undulate apices; margins entire or subentire, at times with distantly serrulate apices, plane, not decurrent; costae very short and double or absent; cells smooth, thin-walled, linear-flexuose to fusiform; basal cells enlarged, broadly long-rectangular; alar cells not differentiated. Synoicous. Setae elongate, smooth. Capsules inclined to arcuate, asymmetric, short-cylindric, neck well developed; exothecial cells collenchymatous; stomata rudimentary, 3–5-celled, on neck; opercula conic-rostrate; annuli of 7–8 rows of thin-walled, quadrate cells, persistent at the base of the opercula; peristome diplolepideous, exostome narrowly triangular, median furrow present, dorsal (outer) surface densely and closely cross-striate and papillose below; endostome lightly papillose, basal membranes high, segments broad, keeled, weakly perforate, cilia absent or rudimentary. Calyptrae mitrate, irregularly lobed at base, naked, smooth.

Philophyllum is a monospecific genus restricted to the Neotropics, where it occurs sporadically in Brazil, Peru, and Guatemala. The genus has only been found in bromeliad tanks. Its large, ovate-lanceolate leaves have piliferous acumina; entire to obscurely serrulate margins; mostly short, double costae; and smooth, thin-walled, linear-flexuose median cells. Sporophytically it has elongate setae and inclined capsules with collenchymatous exothecial cells, rudimentary stomata, and a hookeriaceous peristome. As in many other Hookeriaceae genera, *Philophyllum* has a specialized, massive annulus that consists of numerous rows of thin-walled, quadrate cells that are persistent at the base of the opercula. All *Philophyllum* collections examined in this study had mitrate calyptrae, but Buck (1992) attributed the occasional presence of a cucullate-like calyptra to the genus. His description of the cucullate calyptrae ("when cucullate ... irregularly shallowly lobed at base"), however, appears similar to the poorly developed mitrate calyptrae that often occur in some *Macromitrium* species. In *Macromitrium* this odd calyptra appears to be a modified mitrate calyptra that is deeply split along one lobe and shallowly split along the others. The genus has been placed in the Leucomiaceae (Buck

1992), with which it shares a similar leaf areolation, but the presence in the leaves of short, double costae as well as mitrate calyptrae indicates *Philophyllum* is misplaced there. Buck *et al.* (2005), on the basis of molecular evidence, transferred *Philophyllum* to the Pilotrichaceae *sensu lato* and positioned it near *Stenodictyon pallidum*. The genus was revised by Buck (1992).

The name *Philophyllum* combines the Greek *philo-* (love or fond of) with *phyllon* (leaves), in reference to its odd habitat: submerged at the base of bromeliad leaves.

Philophyllum tenuifolium (Mitt.) Broth., Nat. Pflanzenfam. I(3): 945. 1907. *Hookeria tenuifolia* Mitt., J. Linn. Soc., Bot. 12: 359. 1869. *Hookeriopsis tenuifolia* (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 361. 1877. Protologue. Brasilia tropica, *Burchell.*

Hookeria lorifolia Hampe, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn, ser. 3, 6: 160. 1874 [1875]. *Callicostella lorifolia* (Hampe) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 356. 1877. *Philophyllum lorifolium* (Hampe) Broth. *ex* Paris, Coll. 23. 1909. Protologue. [Brazil] Sub *Nr. 7290.* [In vicinia urbis Rio de Janeiro, lecti *A. Glaziou.*]

Philophyllum bromeliae Müll. Hal., Bull. Herb. Boissier 6: 123. 1898. Protologue. Brasilia, Serra Itatiaia, 2300 m altum, in foliis Bromeliaceae, Febr. 1894 c. fr. maturis: *E. Ule*, Coll. *N^o^ 1860.*

Philophyllum bromeliophilum Müll. Hal., Hedwigia 39: 285. 1900. Protologue. Brasilia, insula Sa. Catharina, monte Flaggenberg, Augusto 1886: *E. Ule*, Coll. *No. 125.*

Plants medium-sized, glossy, pale green, yellowish green, or reddish brown, in loose mats. Stems prostrate, simple or irregularly branched, 2–4 cm long, hyaline to pale green when young, becoming red with age, complanate-foliate; young stems in cross section with outer cells smaller than the inner cells, otherwise cells thin-walled and undifferentiated, old stems in cross section with epidermis of 1–2 rows of small, thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2 cells long, basal cell short-rectangular, reddish brown, upper cell elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, not or sparsely and irregularly branched. Leaves flattened, lateral leaves spreading, dorsal and ventral leaves erect to erect-spreading, laxly crispate when dry, flaccid when wet, somewhat distantly spaced, ovate-lanceolate, 3–4 mm long, asymmetric, gradually narrowed to long or piliferous, flexuose or undulate apices; margins entire or subentire, at times with distantly serrulate apices, plane, not decurrent; costae very short and double or absent; cells smooth, thin-walled, linear-flexuose to fusiform, 80–140 × 10–14 μm; basal cells enlarged, broadly long-rectangular; alar cells not differentiated. Synoicous. Setae elongate, red, flexuose, 1–3 cm long, smooth, at times somewhat roughened below capsules. Capsules inclined to arcuate, asymmetric, short-cylindric, 1.5–2.5 mm long, neck well developed; exothecial cells rounded to short-rectangular, incrassate, collenchymatous; stomata rudimentary, 3–5-celled, on neck; opercula conic-rostrate, 1.0 mm long; annuli well developed, of 7–8 rows of thin-walled, quadrate cells, persistent at the base of the opercula; peristome diplolepideous, exostome narrowly triangular, dorsal (outer) surface yellow, with broad median furrows, densely and closely cross-striate and papillose below, coarsely papillose above, ventral (inner) surface hyaline to yellowish, smooth to lightly papillose, trabeculae weakly projecting; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, keeled, weakly perforate, cilia absent or rudimentary. Spores rounded to oval, 18–24 μm, finely papillose. Calyptrae mitrate, 1.5–2.0 mm long, irregularly lobed at base, naked, smooth.

Illustrations. Brotherus (1907a, Fig. 689); Brotherus (1925, Fig. 620); Bartram (1949, Fig. 143 E–H); Welch (1974, Figs. 425–431); Gradstein *et al.* (2001, Fig. 150 A–F). Figure 205.

Habitat. Submerged in bromeliad tanks; 1200–2100 m.

Distribution in Central America. GUATEMALA. Alta Verapaz: *Steyermark 43890* (F, FH, NY).

World range: Central America; Western South America, Brazil.

Philophyllum tenuifolium is a medium-sized species that can be immediately recognized by its habitat: submerged or floating at the base of bromeliad leaves. Its plants are pale green, with leaves that are flaccid when wet, but crispate-contorted when dry. The stems have been described as having somewhat larger cells toward the center, but otherwise lacking internal differentiation (Buck 1992). This, however, is true only for young stems; as they age the stems develop an epidermis of thick-walled

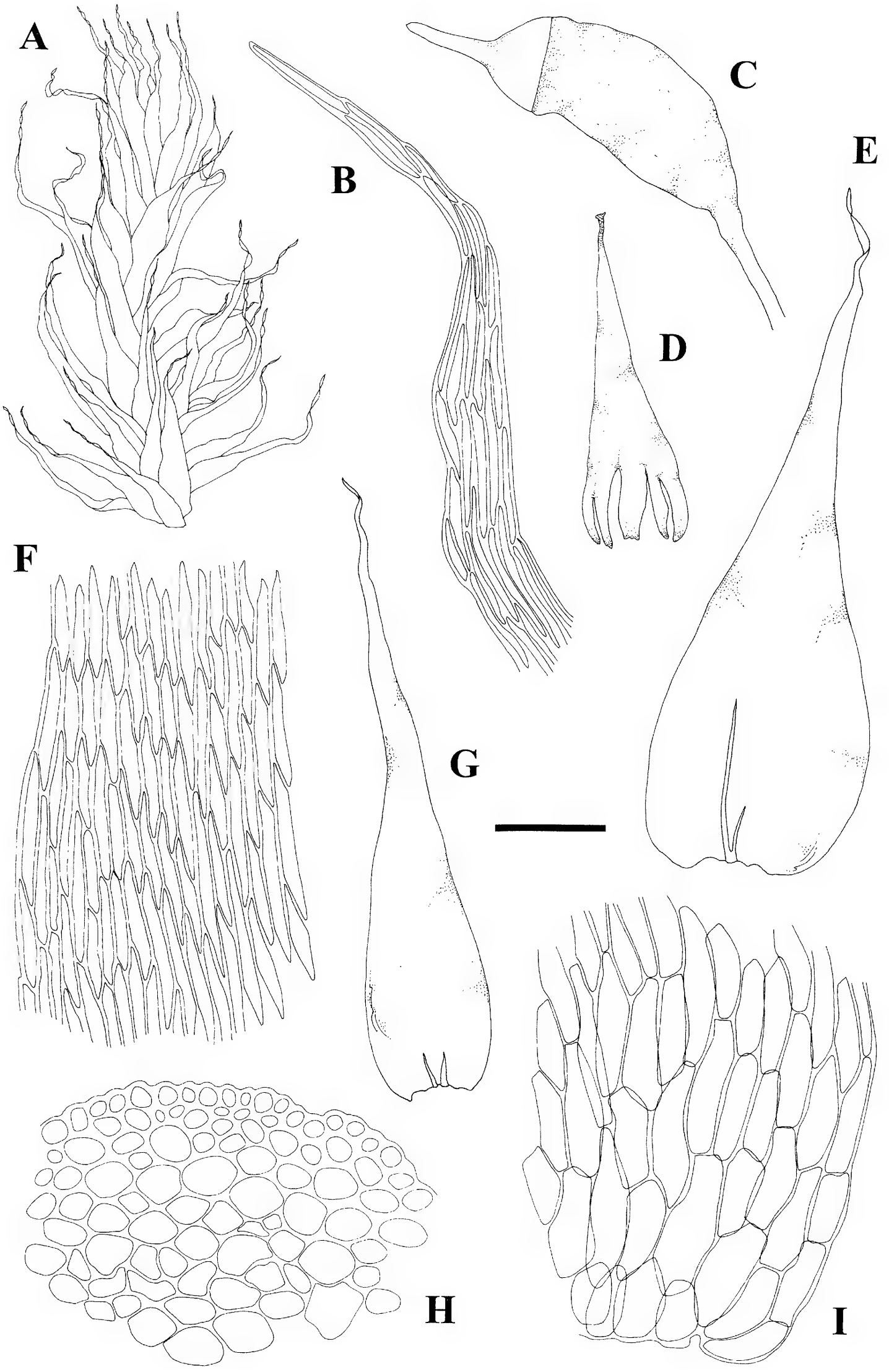
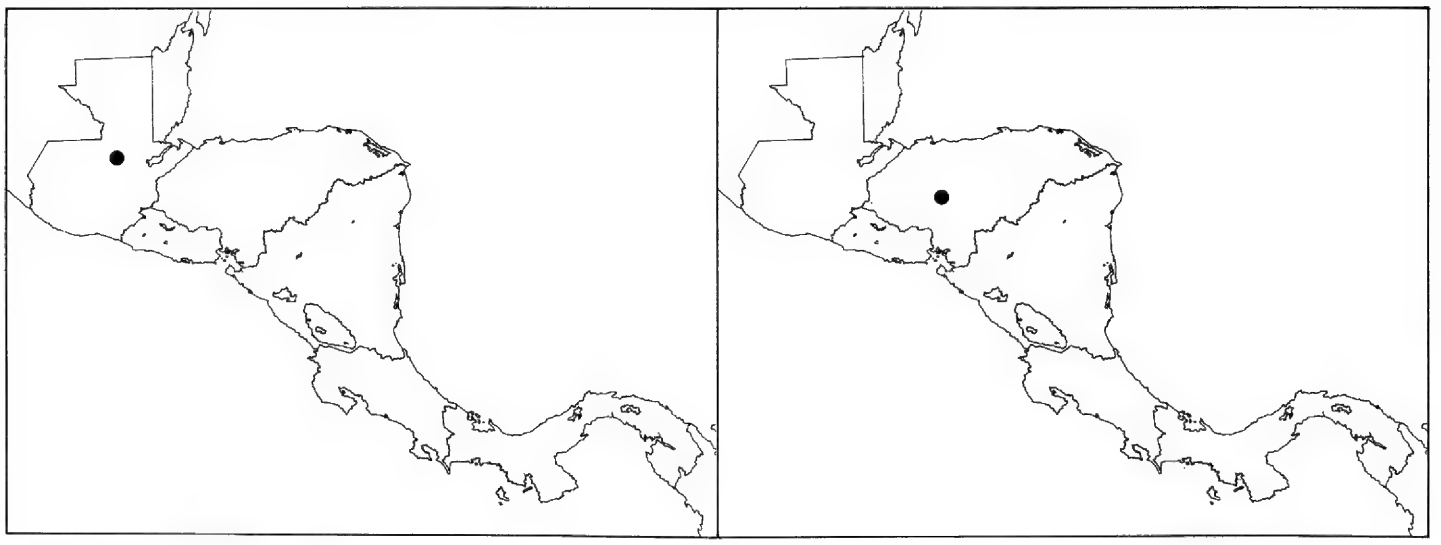


Figure 205. *Philophyllum tenuifolium*. A. Habit. B. Leaf apex. C. Seta, capsule, and operculum. D. Calyptra. E & G. Leaves. F. Median leaf cells and margin. H. Stem in cross section. I. Basal and alar cells. Scale in mm: bar = 0.08 (H); bar = 0.09 (B, F, I); bar = 0.6 (D); bar = 0.7 (C, E, G); bar = 1.96 (A). H from *Timme 6357*; all other figure parts from *Steyermark 43890*.



Philophyllum tenuifolium *Pilotrichidium antillarum*

cells. *Philophyllum tenuifolium* has large, ovate-lanceolate leaves with long, filiform acumina, smooth to subentire or obscurely serrulate margins, and smooth cells that are linear-flexuose above, enlarged, broadly rectangular at base, and lack alar cell differentiation. Most leaves have short, double costae, but occasionally they are ecostate. The species is synoicous, and all collections examined from Central and South America had typical hookeriaceous sporophytes: elongate setae; collenchymatous exothecial cells; rudimentary stomata; massive, persistent annulus; and hookeriaceous peristome. All collections examined for this study had mitrate calyptrae that are irregularly and deeply lobed at base.

In Central America the only species that could be confused with *Philophyllum tenuifolium* are *Leucomium strumosum* or *Hookeria acutifolia*, because all three species have leaves with a similar areolation. *Leucomium strumosum*, however, differs from *P. tenuifolium* in having shorter (1–3 mm long), absolutely ecostate, consistently entire leaves and well-formed cucullate calyptrae. *Hookeria acutifolia* differs in having ovate to oblong-ovate, typically bluntly acute leaves that are ecostate or have a bistratose region only at the very base.

13. *Pilotrichidium* Besch., Ann. Sci. Nat., Bot., sér. 6, 3: 243. 1876.

Plants medium-sized to large, dark green, yellow green, to reddish brown, dull, rigid. Stems creeping or erect-ascending, irregularly to subpinnately, variously complanate-foliate; stems in cross section with a hyalodermis, subepidermal layer of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions at base of costae, not or sparsely and irregularly branched. Leaves often flattened, oblong, oblong-ovate, or rectangular-oblong, frequently dimorphic, extremely variable in shape, apices truncate, broadly obtuse to long-acute, shortly rounded to the insertions; cells pluripapillose throughout or smooth below and minutely papillose above by 1–3 papillae, firm-walled, marginal cells sometimes forming an indistinct border of linear-rectangular, incrassate, porose cells; margins entire, frequently erect to inflexed on one side below; costae double, very strong, smooth, prominent at back, at times converging toward the tips, 3/4 or more the leaf length, usually projecting as two dorsal spines. Asexual gemmae occasionally present, 2–3-celled, hyaline, on reddish brown, branching stalks abaxial to the leaf insertions at base of costae. Dioicous. Setae elongate, smooth. Capsules erect or horizontal to pendent, oblong; opercula conic rostrate; annuli well developed; peristome diplolepideous, exostome narrowly triangular, median furrow present or absent, dorsal (outer) surface red or yellow, trabeculae projecting laterally, densely and closely cross-striate below, coarsely papillose above; endostome as long as the exostome, pale yellow to hyaline, smooth to lightly papillose, basal membranes high, segments broad, keeled, at times perforate, cilia absent. Calyptrae mitrate, lobed at base, naked.

Pilotrichidium is a Neotropical genus of two species found in the Caribbean and from southern Mexico through Central America to northwestern South America. Plants of *Pilotrichidium* are fairly large, and they often occur in sizable, dense mats. Its stems are variously complanate-foliate and have a distinct hyalodermis. The leaves in *Pilotrichidium* are dimorphic, with asymmetric lateral leaves and symmetric dorsal/ventral leaves that vary in shape from oblong, oblong-ovate, to rectangular-oblong. The leaves have broadly rounded to truncate apices; margins at times obscurely bordered below and entire throughout; very strong double costae that end near the apex where they stoutly project at the tips; and small, irregularly shaped, incrassate upper and median cells that are either pluripapillose throughout or near the leaf apices. *Pilotrichidium* is dioicous, and sporophytes are rarely encountered. The capsules of one *Pilotrichidium* species have a large annulus, and at least one species has rudimentary, multicellular stomata. *Pilotrichidium antillarum* has a typical hookeriaceous peristome, but in *P. callicostatum* the exostome lacks a median furrow. The exothecial cells can be either collenchymatous or evenly thickened. The calyptrae are mitrate, lobed at base, and naked.

In Central America *Pilotrichidium* closely resembles *Callicostella*, especially in leaf shape. Indeed, Allen and Crosby (1986a) speculated that *Pilotrichidium* might only be a weak segregate of *Callicostella* (as *Schizomitrium*). The two can be separated on the basis of the following gametophytic features. In *Pilotrichidium* the leaf margins are entire; the leaf cells are extremely incrassate, irregular in shape, and at least some are pluripapillose; the stem has a hyalodermis; and the costae, which are exceedingly strong, project as stout dorsal spines. In *Callicostella* the leaf margins are usually serrate to dentate above; the cells are thin- to moderately thick-walled, regular in shape, and either smooth or unipapillose; the stem has a sclerodermis; and the weaker costae usually do not stoutly project as spines.

Thamniopsis is a large and unwieldy genus that is similar to *Pilotrichidium* in having a stem hyalodermis. In addition some species of *Thamniopsis* have strong costae that project at the tips, some have entire leaf margins, and some have incrassate, irregularly shaped, papillose leaf cells. No species of *Thamniopsis*, however, has entire leaf margins and pluripapillose leaf cells. Allen and Crosby (1986a) revised the genus *Pilotrichidium*.

The name *Pilotrichidium* combines the generic name *Pilotrichum* and the Greek substantival suffix *-idium* (indicating small).

1. Leaf cells (except those at extreme apex) smooth; setae 17–35 mm long; exostome teeth red, strongly furrowed . . . . . 1. *P. antillarum*
1. Leaf cells pluripapillose throughout; setae 8–12 mm long; exostome teeth yellow, not furrowed . . . . . 2. *P. callicostatum*

1. *Pilotrichidium antillarum* Besch., Ann. Sci. Nat., Bot., sér. 6, 3: 243. 1876. Protologue. Guadeloupe: lieux élevés humides (*L'Herminier*, 1892, *n^{os} 13 et 44*); sur les arbres, forêt de la Découverte (*Husnot, n^{o} 160^{a} ex parte*). Types (see Allen & Crosby 1986a). *L'Herminier 13* (BM, lectotype; H, isolectotype). *L'Herminier 44* (BM, syntype). *Husnot 160 ex parte* (BM, H, syntypes).

Pilotrichidium brunnescens Besch., Ann. Sci. Nat., Bot., sér. 6, 3: 244. 1876. *Hookeria brunnescens* Schimp. *in* Besch., Ann. Sci. Nat., Bot., sér, 6. 3: 244. 1876, invalid name, in synonymy. Protologue. Guadeloupe (*L' Herminier*; *Husnot, n^{o} 171, ex parte*). Types (see Allen & Crosby 1986a). *L'Herminier* (BM, lectotype; BM, NY, isolectotypes). *Husnot 171 ex parte* (BM, syntype).

Pilotrichidium antillarum Besch. var. *complanatum* Besch. *in* Paris, Index Bryol. Suppl. 272. 1900, invalid name, lacks a description.

Pilotrichidium antillarum Besch. var. *cubense* Thér., Mem. Soc. Cub. Hist. Nat. "Felipe Poey" 14: 363. 1940. Protologue. [Cuba] Pico Turquino (*Acuña 354*), (*Léon 11,234*). Types (see Allen & Crosby 1986a). *Léon 11234* (NY [2], lectotypes; FH, US, isolectotypes). *Acuña 354* (FH, PC, syntypes).

Plants medium-sized to large, to 7 cm long, dark green, yellow brown to brownish red, in dull, stiff mats. Stems prostrate, irregularly to subpinnately branched, weakly complanate-foliate; stems in cross section with hyalodermis, subepidermal sclerodermis of 2–5 rows of cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids

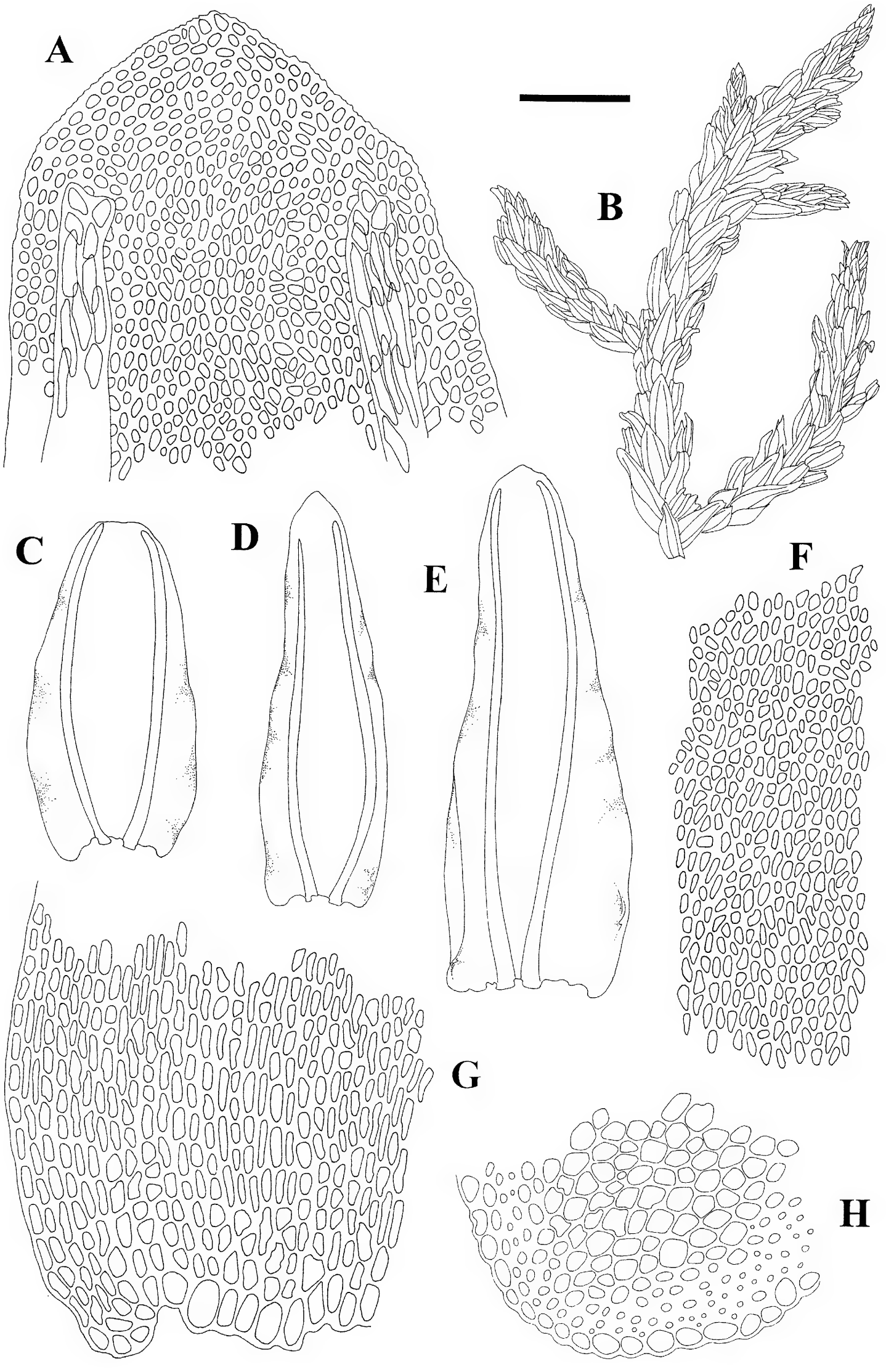


Figure 206. *Pilotrichidium antillarum*. A. Leaf apex. B. Habit. C. Dorsal leaf. D & E. Lateral leaves. F. Median leaf cells. G. Basal and alar cells. H. Stem in cross section. Scale in mm: bar = 0.05 (A, F, G); bar = 0.08 (H); bar = 0.36 (C–E); bar = 1.96 (B). B from *Hegewald & Hegewald 9326*; H from *Duss 14*; all other figure parts from *L'Herminier 13* (type).

from clusters of initials abaxial to the leaf insertions at base of costae, lightly roughened, reddish brown, not or sparsely and irregularly branched. Leaves weakly flattened, erect-spreading, irregularly incurved when dry, loosely appressed when wet, frequently dimorphic. Lateral leaves oblong to oblong-ovate, 1–2 × 0.4–0.7 mm, asymmetric, narrowly to broadly acute, obtuse, or truncate above, mucronate or apiculate, rounded to the insertions; margins entire below, roughened at apex by papillae, erect to inflexed on one side below, otherwise plane, at times with an indistinct border of to 17 rows of narrowly rectangular to linear cells; costae double, strong, smooth, prominent at back, ending 3/4 the leaf length or just below the apex, projecting as two dorsal spines, the spines sometimes reaching beyond the apex; cells at the extreme apex with 1–3 minute papillae, otherwise smooth, upper and median cells irregularly oblong-rounded, quadrate, triangular, or polygonal, incrassate, at times porose, 5–20 × 3–5 µm, lower cells rectangular to linear-rectangular, incrassate and porose, 10–60 µm long; alar cells not differentiated. Dorsal and ventral leaves appressed, oblong-ovate, symmetric; apex more sharply acute than in lateral leaves; basal margins plane to erect, not broadly inflexed; cells less porose, otherwise similar to lateral leaves. Asexual gemmae absent. Dioicous. Setae elongate, 17–30 mm long, red to red brown, smooth. Capsules horizontal to pendent, oblong, 1.2–1.7 mm long, neck well developed, indistinctly scabrous at base; exothecial cells quadrate in 2–4 rows at mouth, those below rectangular, firm- to thick-walled throughout, not collenchymatous; stomata rudimentary, 3–5-celled on neck; opercula conic-rostrate, 1 mm long; annuli well developed; peristome diplolepideous, exostome narrowly triangular, median furrow well developed, dorsal (outer) surface red to red brown, trabeculae projecting laterally, densely and closely cross-striate below, coarsely papillose above; endostome as long as the exostome, pale yellow to hyaline, smooth to lightly papillose, basal membranes high, segments broad, keeled, perforate, cilia absent. Spores 10–18 µm, smooth. Calyptrae mitrate, to 2 mm long, lobed at base, naked.

Illustrations. Thériot (1940, Pl. 54 9a–d); Crosby (1969a, Figs. 6–10, 13, 199, 210, 211, 214); Allen and Crosby (1986a, Figs. 8–17, 19, 20); Duarte Bello (1997, Pl. 250); Buck (1998, Pl. 25 9–16). Figure 206.

Habitat. On rocks and tree trunks, often along streams; 500–1000 m.

Distribution in Central America. HONDURAS (?). *J. Galmansson* (BM).

World range: Central America; Caribbean.

Pilotrichidium antillarum is a fairly large, dark green species that is often found on rocks near streams and grows in large, stiff mats. It has a well-developed stem hyalodermis and somewhat complanate-foliate leaves with stout double costae that often strongly project at the tips. Its leaves are often dimorphic, with erect-spreading, asymmetric lateral leaves and appressed, symmetric dorsal and ventral leaves. The lateral leaves are usually more broadly rounded at the apex and have more strongly porose leaf cells than the dorsal and ventral leaves. The leaf margins are entire except near the extreme apex where they are papillose-roughened. At times the leaf margins are bordered at base by several rows of narrowly rectangular to linear cells. The upper leaf cells in *P. antillarum* are small, irregularly oblong-rounded, quadrate, triangular, or polygonal, incrassate, and smooth except at the extreme apex.

The leaves of *Pilotrichidium callicostatum* differ from those of *P. antillarum* in having more broadly truncate apices, less incrassate and porose cells, and consistently pluripapillose rather than smooth cells. In addition, the setae of *P. callicostatum* are shorter than those of *P. antillarum* (8–12 mm vs. 17–35 mm) and the yellowish exostome lacks a median furrow. In Central America *Pilotrichidium antillarum* has the same overall aspect as *Callicostella*, and both have similarly shaped leaves. *Callicostella* differs from *P. antillarum* in having a stem sclerodermis rather than a hyalodermis, foliose pseudoparaphyllia, and weaker costae.

The single Central American collection of *Pilotrichidium antillarum* has a handwritten label giving only "San Salvador, Honduras" as its locality. There is no town by that name in Honduras; the specimen may have come from San Salvador, the capital of El Salvador. *Pilotrichidium antillarum* and *P. callicostatum* also occur in the Caribbean, but unlike the situation in Central America, *P. antillarum* is the more common species. In the Caribbean *P. antillarum* is found on all the major islands except Jamaica and Trinidad, while *P. callicostatum* is found only on those two islands.

2. *Pilotrichidium callicostatum* (Müll. Hal.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 357. 1877. *Hookeria callicostata* Müll. Hal., Syn. Musc. Frond. 2: 216. 1851. Protologue. Insula antillarum Trinidad, ubi monte Tocuche sterilem legit *Crüger* 1847. Januar. 20. Types (see Allen & Crosby 1986a). Trinidad, *Crüger* 1847 (NY, lectotype; BM, H, MICH, isolectotypes).

Plants medium-sized to large, 1–3 cm long, glaucous green to yellow green, in dull, stiff mats. Stems prostrate, irregularly to subpinnately branched, weakly complanate-foliate; stems in cross section with hyalodermis, subepidermal sclerodermis of 3–4 rows of cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves weakly flattened, erect-spreading, irregularly incurved when dry, rectangular-oblong to oblong-ovate, 1.0–1.8 × 0.4–0.6 mm, symmetric or weakly asymmetric, sides more or less parallel, apex broadly truncate, occasionally obtuse or acute, mucronate, or emarginate; margins roughened throughout by papillose cells, erect to inflexed on one side below, otherwise plane, at times with an indistinct border of to 14 rows of narrowly rectangular to linear cells; costae double, strong, smooth, prominent at back, ending just below the apex, projecting as two dorsal spines; cells pluripapillose throughout, upper and median cells irregularly quadrate, pentagonal, or hexagonal, incrassate, not or rarely porose, 5.0–12 × 2.5–5.0 µm, lower cells linear-rectangular, rectangular, to quadrate, incrassate, at times porose, 7.5–50 µm long, cells across the insertions enlarged, reddish; alar cells not differentiated. Asexual gemmae occasional, 2–3-celled, hyaline, on reddish brown, branching stalks abaxial to the leaf insertions at base of costae. Dioicous. Setae elongate, 8–12 mm long, red to red brown, smooth. Capsules erect, oblong, 1.3 mm long, neck well developed, scabrous at base; exothecial cells reddish, quadrate in 2–4 rows at mouth, those below oval to oblong, collenchymatous; stomata not seen; opercula conic-rostrate, 1.0–1.2 mm long; annulus not seen; peristome diplolepideous, exostome narrowly triangular, median furrow absent, median lines distinct, dorsal (outer) surface light yellowish, trabeculae slightly projecting laterally, densely and closely cross-striate below, coarsely papillose above, ventral (inner) surface dark yellow, secondary deposition narrow but thick, lightly papillose; endostome as long as the exostome, yellow, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not or faintly perforate, cilia absent. Spores 12–14 µm, smooth. Calyptrae mitrate, 1 mm long, yellowish, irregularly lobed at base, naked.

Illustrations. Crosby (1969a, Figs. 209, 212, 213); Allen and Crosby (1986a, Figs. 1–7, 18); Sharp *et al.* (1994, Fig. 624); Buck (1998, Pl. 25 1–8); Gradstein *et al.* (2001, Fig. 169 A–E). Figure 207.

Habitat. On tree trunks and roots, rotting logs, and rocks; 350–1500 m.

Distribution in Central America. COSTA RICA. Heredia: *Crosby & Crosby 6064* (MO); Puntarenas: *Lyon 417* (MO). PANAMA. Bocas del Toro: *Allen 5602* (MO); Chiriquí: *McPherson 6824A* (MO); Coclé: *Crosby 4424* (MO); Darién: *Allen 8915A* (MO); Veraguas: *Crosby 10167* (MO).

World range: Mexico; Central America; Caribbean; Western and Northern South America.

Pilotrichidium callicostatum is a medium-sized to large, dark green species. It has a well-developed stem hyalodermis and complanate-foliate leaves with stout double costae that strongly project at the tips. Its rectangular-oblong to oblong-ovate leaves are variously, at times strongly, dimorphic: dorsal and lateral leaves symmetric with truncate apices and weakly convergent costae; ventral leaves asymmetric with acute apices and strongly convergent costae. The leaf margins are roughened throughout by papillose cells and are weakly bordered at base by several rows of narrowly rectangular to linear cells. The upper leaf cells in *P. callicostatum* are small, irregularly quadrate, pentagonal, or hexagonal, incrassate, and pluripapillose throughout. In a single collection of *P. callicostatum* from Panama (*Crosby 10153*, MO), 1- to 2-celled brood bodies have been observed. These brood bodies are borne on reddish brown, branched stalks at the leaf insertions opposite the dorsal surface of the costae. The brood body initials occur in the same place and appear to be identical to the rhizoidal initials. Brood bodies of this type and in this position are a commonly encountered feature of the Hookeriaceae.

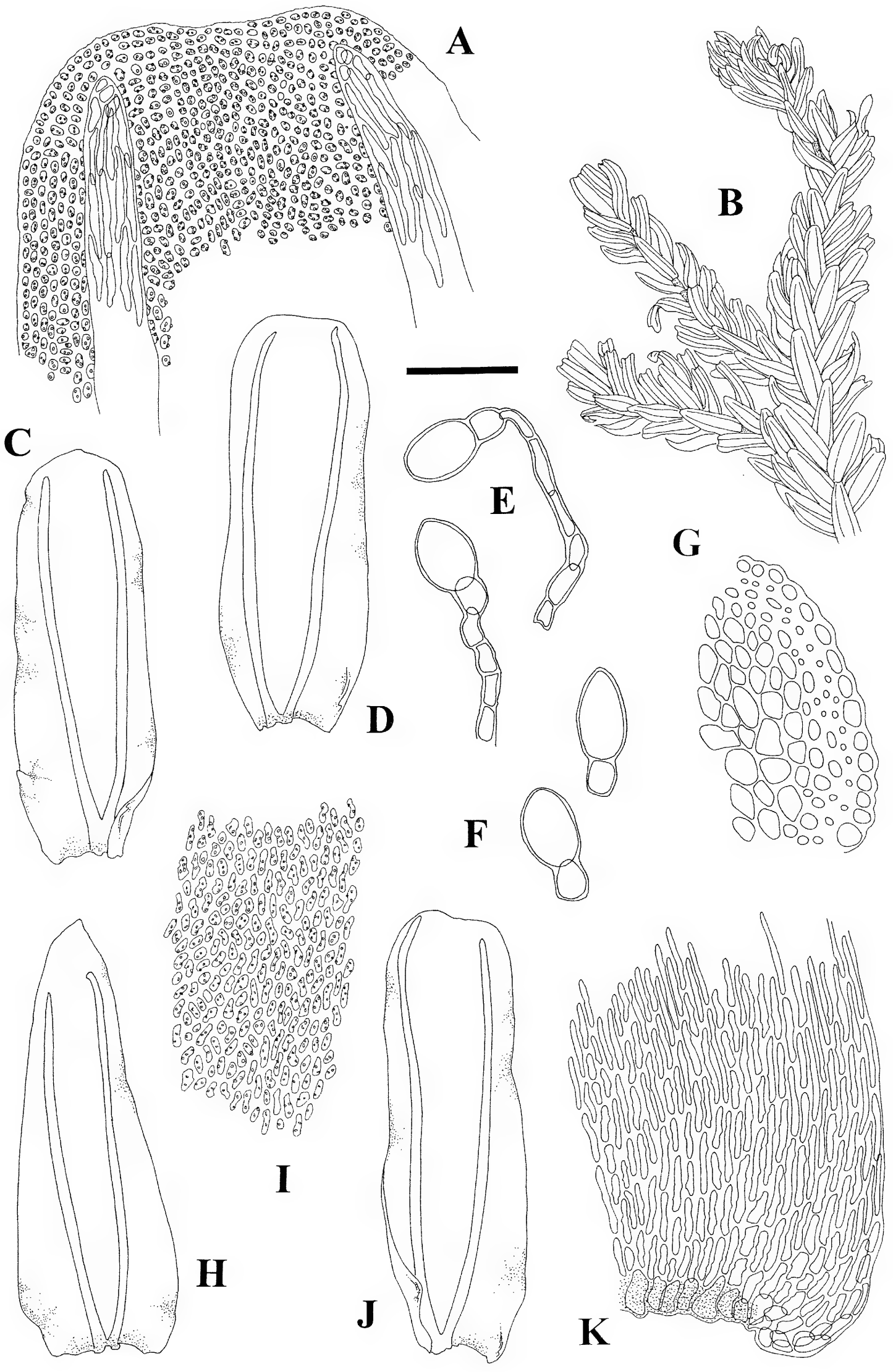
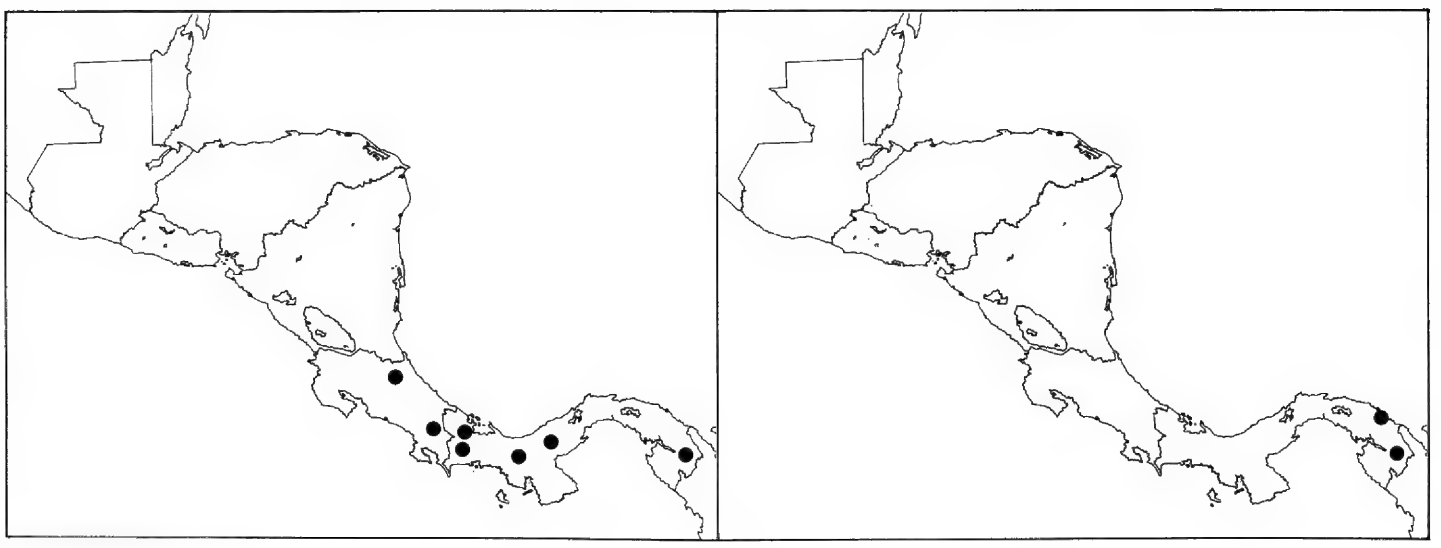


Figure 207. *Pilotrichidium callicostatum*. A. Leaf apex. B. Habit. C, D & J. Lateral and dorsal leaves. E. Stalked gemmae. F. Detached gemmae. G. Stem in cross section. H. Ventral leaf. I. Median leaf cells. K. Basal and alar cells. Scale in mm: bar = 0.06 (A, E–G, I, K); bar = 0.28 (C, D, H, J); bar = 1.56 (B). A from *Crüger* (type); E, F, I, K from *Crosby 10153*; all other figure parts from *Allen 5596*.



Pilotrichidium callicostatum *Stenodesmus tenuicuspis*

Pilotrichidium antillarum differs from *P. callicostatum* in having acute to narrowly rounded leaf apices; more incrassate and porose leaf cells; and leaf cells that, except for those at the leaf tip, are smooth. In addition, the setae of *P. antillarum* are considerably longer than those of *P. callicostatum* (17–35 mm vs. 8–12 mm), and the red exostome teeth are strongly furrowed.

In Central America *Pilotrichidium callicostatum* has the same overall aspect as *Callicostella* and both have broadly truncate leaves. *Callicostella* differs from *P. callicostatum* in having a stem sclerodermis rather than a hyalodermis, foliose pseudoparaphyllia, weaker costae, smooth or unipapillose leaf cells, and strongly furrowed exostome teeth.

14. *Stenodesmus* (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 358. 1877.
Hookeria Sm. sect. *Stenodesmus* Mitt., J. Linn. Soc., Bot. 12: 347. 1869.

Plants medium-sized, green, reddish, yellowish, or yellow brown, in mats. Stems prostrate or ascending, irregularly to subpinnately branched, hyaline to yellowish when young, becoming reddish with age, evenly foliate; stems in cross section with hyalodermis, 1–2 layers of small, thick-walled subepidermal cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves monomorphic, erect to erect-spreading when dry, erect-spreading when wet, ovate to oblong, symmetric, abruptly constricted to piliferous acumina, concave; margins entire throughout or subentire in upper 1/4, plane to erect, not bordered; costae double, thin, ending 2/3 the leaf length, diverging throughout, usually unequal, smooth at back, not projecting at the apices; cells smooth, thin-walled, upper cells linear-hexagonal to oblong-rectangular, lower cells oblong-rectangular to long-rectangular, bulging, cells across the insertions short-rectangular, reddish; alar cells not differentiated. Dioicous. Setae elongate, densely spinose above, spiculose-papillose at base. Capsules erect to somewhat inclined, ovoid, neck well developed; exothecial cells collenchymatous; stomata rudimentary, 3–6-celled, on neck; opercula long-conic; annuli rudimentary; peristome diplolepideous, exostome narrowly triangular, median furrow absent, dorsal (outer) surface broad, whitish yellow, lightly papillose throughout, trabeculae thin, median lines faint, ventral (inner) surface narrow, 1/3 or less the width of the dorsal surface, dark yellow to red, lightly papillose, deposition thick; endostome as long as the exostome, pale yellowish, lightly papillose throughout, basal membranes high, segments broad, concave-keeled, not perforate, cilia absent. Calyptrae campanulate-mitrate, irregularly lobed at base, with a few multicellular hairs.

Stenodesmus is a monospecific Neotropical genus restricted to southern Central America and northern South America. Plants of *Stenodesmus* are medium in size, pale green, green, or yellowish red in color, and evenly foliate; the stems have a distinct hyalodermis. The leaves in *Stenodesmus* are symmetric, monomorphic, ovate to oblong, and smooth when dry; abruptly constricted above into

long piliferous acumina; and elimbate, with margins either entire throughout or with subentire acumina. The leaves have weakly developed, smooth costae that end somewhat above midleaf, diverge throughout, and do not project at the tips; long-hexagonal upper and median cells that are extremely variable in width; and enlarged, at times bulging, and thin-walled basal cells. The leaf cells are smooth throughout and enlarged in a reddish band across the line of insertion. *Stenodesmus* has long-conic opercula that curiously are more or less the same size as the ovoid capsules. This odd situation is also encountered in *Ochrobryum* (Leucobryaceae) but otherwise is rare. *Stenodesmus* has spinose setae, rudimentary stomata consisting of 3–6 cells, and a daltoniaceous peristome. The calyptrae are campanulate-mitrate, irregularly lobed at base, and with sparse multicellular hairs.

In Central America *Stenodictyon* and *Stenodesmus* are gametophytically identical, and sterile plants are impossible to place with confidence. Their sporophytes, however, are radically different; those of *Stenodictyon* differ from those of *Stenodesmus* in having smooth setae, conic-rostrate opercula, oblong-cylindric capsules, and hookeriaceous peristomes. *Thamniopsis* is also gametophytically similar to *Stenodesmus*. Both genera have a stem hyalodermis, and there are some *Thamniopsis* species with ovate to oblong leaves that are abruptly constricted above into long, narrow apices. These *Thamniopsis* species differ from *Stenodesmus* in having serrate leaf margins, smooth setae, conic-rostrate opercula, cylindric capsules, and hookeriaceous peristomes.

Lepidopilum and *Stenodesmus* have identical sporophytes, and both genera also have a stem hyalodermis. The gametophytes of many *Lepidopilum* species differ from *Stenodesmus* in having complanate-foliate stems and asymmetric, distinctly bordered leaves. However, there are some *Lepidopilum* species with evenly foliate, symmetric, elimbate leaves. There are, though, no *Lepidopilum* species with leaves that are abruptly constricted above into long, narrow apices. Whether or not this sole distinguishing feature between the genera is enough to warrant the recognition of two genera is debatable.

The name *Stenodesmus* combines the Greek *stenos* (narrow) with *desmos* (band or something used for tying).

Stenodesmus tenuicuspis (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 358. 1877. *Hookeria tenuicuspis* Mitt., J. Linn. Soc., Bot. 12: 347. 1869. Protologue. [Ecuador] Andes Quitenses, in sylva Canelos (3000 ped.), *Spruce, n. 706.* Types. Andes Quitense, montana de Canelos, *Spruce 706* (G, MO, PC, isotypes).

Plants medium-sized, 2–3 cm long, green, reddish, yellowish, or yellow brown, in mats. Stems prostrate or ascending, irregularly to subpinnately branched, hyaline to yellowish when young, becoming reddish with age, evenly foliate; stems in cross section with hyalodermis, 1–2 layers of small, thick-walled subepidermal cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves monomorphic, erect to erect-spreading when dry, erect-spreading when wet, ovate to oblong, 1.5–2.2 mm long, symmetric, abruptly constricted to piliferous acumina, concave; margins entire throughout or subentire in upper 1/4, plane to erect, not bordered; costae double, thin, ending 2/3 the leaf length, diverging throughout, usually unequal, smooth at back, not projecting at the apices; cells smooth, thin-walled, upper cells linear-hexagonal to oblong-rectangular, 60–100 × (4–)10–16(–20) µm, lower cells oblong-rectangular to long-rectangular, bulging, cells across the insertions short-rectangular, reddish; alar cells not differentiated. Dioicous. Setae elongate, 12–20 mm long, red, densely spinose above, spiculose-papillose at base. Capsules erect to somewhat inclined, ovoid, 1.5–2.0 mm long, neck well developed; exothecial cells reddish, quadrate to oblate in 2–3 rows at mouth, those below oblong to rectangular, collenchymatous; stomata rudimentary, 3–6-celled, on neck; opercula long-conic, 1–2 mm long; annuli rudimentary, of a few hyaline, thin-walled cells; peristome diplolepideous, exostome very narrowly triangular, median furrow absent, dorsal (outer) surface broad, whitish yellow, lightly papillose throughout, trabeculae thin, median lines faint, ventral (inner) surface narrow, 1/3 or less the width of the dorsal surface, dark yellow to red, lightly papillose, deposition thick; endostome as long as the exostome, pale yellowish, lightly papillose throughout, basal membranes high, segments broad, concave-keeled, not perforate, cilia absent. Spores rounded, 12–20 µm, lightly pa-

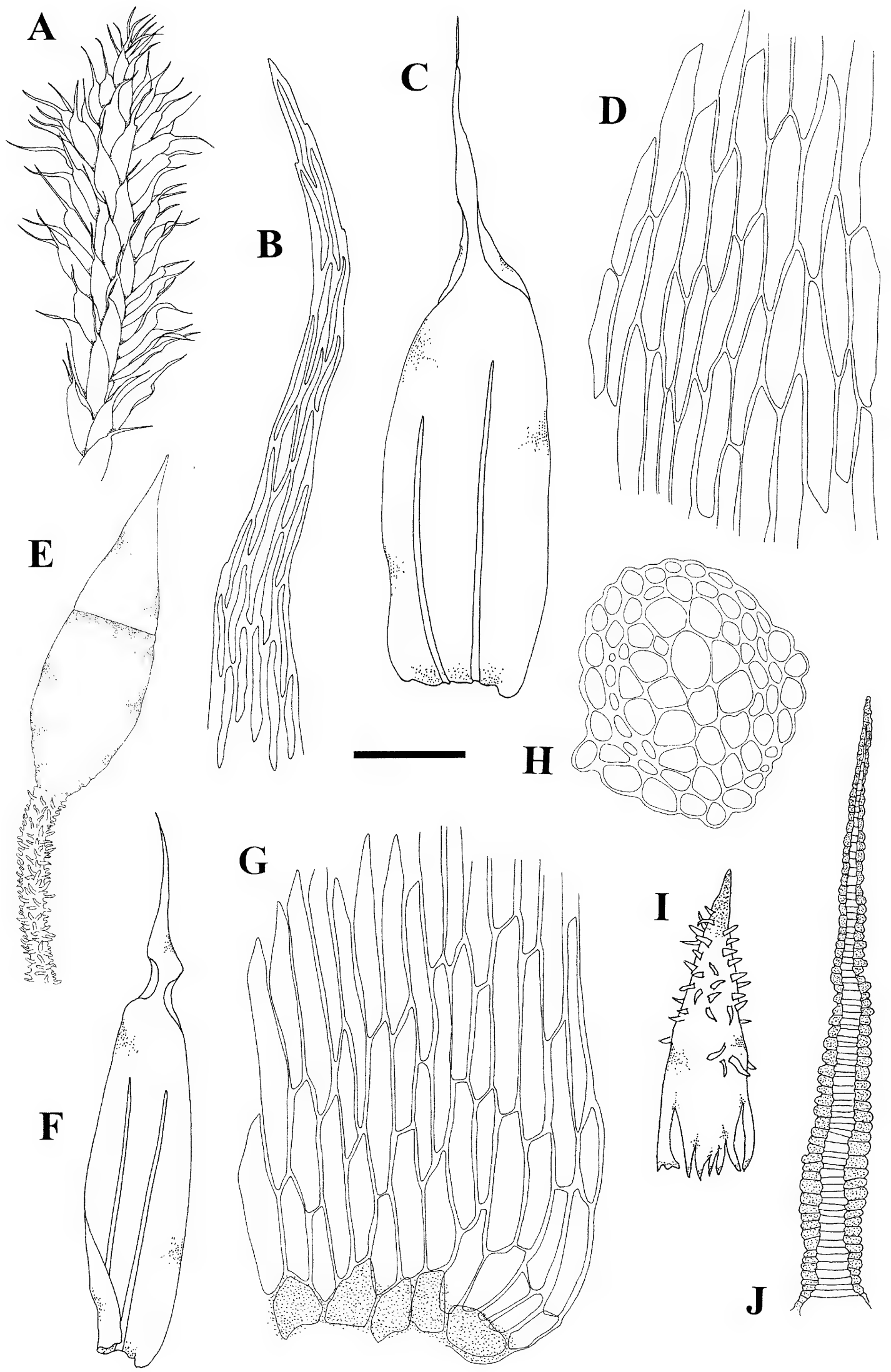


Figure 208. *Stenodesmus tenuicuspis*. A. Habit. B. Leaf apex. C & F. Leaves. D. Median leaf cells. E. Seta, capsule, and operculum. G. Basal and alar cells. H. Stem in cross section. I. Calyptra. J. Exostome, ventral (inner) surface. Scale in mm: bar = 0.06 (B, D, G); bar =0.08 (H); bar = 0.2 (J); bar = 0.4 (C, F); bar = 1.3 (E, I); bar = 1.96 (A). A, C, D, J from *Spruce 706* (type); B, F from *Sytsma 2746*; all other figure parts from *Ramírez 8314*.

pillose. Calyptrae campanulate-mitrate, 3–4 mm long, reddish yellow, irregularly lobed at base, with a few multicellular hairs.

Illustrations. Brotherus (1907a, Fig. 696); Brotherus (1925, Fig. 618); Gradstein *et al.* (2001, Fig. 169 F–I). Figure 208.

Habitat. On tree branches; 650–762 m.

Distribution in Central America. PANAMA. Darién: *Folsom 4442* (MO); San Blas: *Sytsma et al. 2746* (MO).

World range: Central America; Western South America.

Stenodesmus tenuicuspis is a small to medium-sized, epiphytic species with prostrate or ascending, evenly foliate stems and leaves that are erect to erect-spreading when dry. Its ovate to oblong leaves have abruptly constricted, long, slender acumina; mostly entire, but occasionally subentire upper margins; and elongate hexagonal cells that are extrememly variable in form (especially width) within single leaves. In some leaves the cells are as narrow as 4 µm, while in others they can be 20 µm wide, but there is complete intergradation between the cell width extremes. The basal cells are enlarged, variously rectangular, and bulging; the cells across the insertions are swollen and light reddish. The costae end in the upper parts of the leaves, but they are thin, smooth at back, and do not project at the tips. The setae of *S. tenuicuspis* are spiculose-papillose at base and densely spinose above.

The gametophytes of *Stenodictyon pallidum* and *S. wrightii* are identical in size, aspect, and microscopic features to those of *Stenodesmus tenuicuspis*. The *Stenodictyon* species tend to have narrower leaf cells than those of *Stenodesmus tenuicuspis*. However, the leaf cells of *Stenodesmus tenuicuspis* are so variable in width that even this distinction fails to separate it from the *Stenodictyon* species. The sporophytes of the *Stenodictyon pallidum* and *S. wrightii*, though, are radically different from those of *Stenodesmus tenuicuspis*: smooth vs. spinose setae; conic-rostrate vs. long-conic opercula; oblong-cylindric vs. ovoid capsules; and hookeriaceous vs. daltoniaceous peristome.

The presence of a stem hyalodermis and monomorphic leaves that are constricted at the base of the acumina are features also found in *Thamniopsis steyermarkii*, the *acicularis*-form of *T. undata*, *T. glandulifera*, and *T. purpureophylla.* These species differ from *Stenodesmus tenuicuspis* in having sharply serrate leaf margins, smooth setae, and hookeriaceous peristomes. *Lepidopilum* also has a stem hyalodermis, and its sporophytic features are identical to those of *S. tenuicuspis.* Most species of *Lepidopilum* differ from *S. tenuicuspis* in having complanate-foliate stems and asymmetric, distinctly bordered leaves. However, there are *Lepidopilum* species with evenly foliate stems and symmetric, elimbate leaves. *Stenodesmus tenuicuspis* differs from these latter species only in having leaves abruptly constricted above into long, narrow apices.

15. *Stenodictyon* (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 358. 1877.
Hookeria Sm. sect. *Stenodictyon* Mitt., J. Linn. Soc., Bot. 12: 348. 1869.

Plants small to medium-sized, pale green, green, yellowish, or yellow red, in mats. Stems prostrate, irregularly branched to subpinnately branched, hyaline to yellowish when young, becoming reddish with age, evenly foliate; stems in cross section with a hyalodermis, sometimes a subepidermal layer of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia small, foliose; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect, erect-patent, erect-spreading, at times lightly undulate or flexuose-contorted when dry, erect-spreading when wet, monomorphic, ovate, oval, or oblong-lanceolate, symmetric, abruptly constricted above to long, slender acumina, concave; margins entire throughout or obscurely sinuate on the acumina, plane to erect, not bordered; costae double, thin, ending 1/3–2/3 the leaf length, diverging throughout, usually unequal, smooth at back, not projecting at the apices; cells smooth, upper cells linear-elongate or long-rhomboidal, firm- or thin-walled, at times porose, lower cells oblong-rectangular to long-rectangular, porose, bulging near insertions, cells across the insertions reddish, short-rectangular, porose; alar cells not differentiated. Asexual propagula fusiform, multicellular, uniseriate, arising on specialized brood branches in terminal clusters or abaxial to the leaf insertions

opposite the costae. Dioicous, autoicous, or paroicous. Setae elongate, red, smooth throughout, at times somewhat roughened below the capsules. Capsules pendent, horizontal, or suberect, oblong-cylindric, neck well developed; exothecial cells quadrate at mouth, those below oblong to rectangular, usually collenchymatous; stomata rudimentary, on neck; opercula conic-rostrate, annuli of several rows of thin-walled cells, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome narrowly triangular with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface dark red, densely and closely cross-striate below, coarsely papillose above, primary walls yellow, smooth, ventral (inner) surface hyaline to yellowish, deposition thin, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not or faintly perforate, cilia absent. Calyptrae mitrate, yellowish, irregularly lobed at base, naked or sparsely hairy.

Stenodictyon is a strictly Neotropical genus with four species of limited (Caribbean, southern Central America, and northern South America) distribution. Plants of *Stenodictyon* are small to medium in size, pale green, green, or yellowish red in color, and they have evenly foliate stems with a distinct hyalodermis. The ovate to oblong-lanceolate leaves are symmetric, monomorphic, usually smooth when dry, and abruptly constricted above into long piliferous acumina. The leaf margins are elimbate and typically entire throughout, but occasionally the acumina can be subentire or sinuate. The weakly developed costae in *Stenodictyon* are smooth at back, do not project at the tips, end at or above midleaf, and diverge throughout. The leaves have smooth cells and typically a heterogeneous areolation, in which the upper and median cells are narrow and firm-walled; the lower cells are enlarged, at times bulging, and usually thin-walled; and the basal cells across the insertions are enlarged in a broad band. The capsules of *Stenodictyon* have the distinctive massive, persistent annulus consisting of multiple rows of yellowish, hexagonal cells that is characteristically found in several other Hookeriaceae genera. As in nearly all other members of the Hookeriaceae, the rudimentary stomata are made up of 2–6 cells. *Stenodictyon* has a typical hookeriaceous peristome. The calyptrae are mitrate, irregularly fringed at base, and sometimes sparsely hairy.

Stenodesmus and *Stenodictyon* have radically different sporophytes, but they are gametophytically identical and likely to be confused. The sporophytes of *Stenodesmus* differ from those of *Stenodictyon* in having spinose setae, long-conic opercula, ovoid capsules, and daltoniaceous peristomes. *Stenodesmus* is a rarely encountered species in Central America, and *Stenodictyon* is more likely to be confused with *Thamniopsis* because both genera have identical sporophytes, stems with a distinct hyalodermis, and a similar heterogeneous leaf areolation. Although many species of *Thamniopsis* differ from *Stenodictyon* in having polymorphic leaves and prorate leaf cells, there are *Thamniopsis* species with monomorphic leaves and smooth leaf cells. Many species of *Thamniopsis* can be distinguished from *Stenodictyon* by their variously serrate (at times bidentate) margins. However, the type of *Thamniopsis* has entire leaves, and although the leaf margins in *Stenodictyon* are typically entire, the acumina can sometimes be subentire or sinuate. Finally, there are some species of *Thamniopsis* with leaves abruptly constricted above into long piliferous acumina in exactly in the same manner as in *Stenodictyon.*

As presently circumscribed *Thamniopsis* is not distinct from *Stenodictyon*. Unfortunately, *Stenodictyon* is the older name and combining the two genera would require a large number of nomenclatural transfers. *Thamniopsis* is a large, unwieldy genus that may be polyphyletic. It is in need of revision in order to clarify its generic boundaries. In the interest of nomenclatural stability it seems best to refrain from making wholesale transfers of *Thamniopsis* species into *Stenodictyon* until *Thamniopsis* has been critically revised.

Allen *et al.* (1986) reviewed the genus *Stenodictyon*, and their generic and family discussions on the genus are useful. The species treatment of *S. wrightii*, however, is severely flawed because it was confused with *Stenodesmus tenuicuspis*, *Thamniopsis steyermarkii*, and *Lepidopilum longifolium*.

The name *Stenodictyon* combines the Greek *stenos* (narrow) with *dictyon* (net).

1. Leaves ovate to oval, 2.0–2.5 × 0.7–1.0 mm . . . . . 2. *S. ovatum*
1. Leaves oblong-lanceolate, 1.0–2.0 × 0.2–0.5 mm 2

2. Plants with propagula in terminal clusters on specialized brood branches . . . . . 1. *S. crosbyi*
2. Plants without propagula or propagula in clusters abaxial to the leaf insertions opposite the costae 3

3. Upper leaf cells linear or elongate-rectangular, 3–6 μm wide, firm-walled, sigmoid; setae 35–50 mm long . . . . . 4. *S. wrightii*
3. Upper leaf cells rhomboidal to long-rhomboidal, 6–14 μm wide, thin-walled, lateral walls straight; setae 8–15 mm long . . . . . [3. *S. pallidum*]

1. *Stenodictyon crosbyi* B. H. Allen, *sp. nov.* Type. Panama. Veraguas: Stream valley 10.4 km along road leading NW from Escuela Agricola "Alto de Piedra," 5.4 km NW of Santa Fe, 08°30′N, 081°05′W, *Marshall R. Crosby 10137* (MO, holotype; PMA, isotype).

Species determinatis terminantibus in massas gemmarum a congeneribus diversa.

Plants medium-sized, 1–2 cm long, light, glossy, yellowish green, in dense tufts. Primary stems prostrate and creeping. Secondary stems weakly ascending, not or sparsely branched, hyaline to yellowish when young, becoming red to red brown with age, evenly foliate; stems in cross section with well-developed hyalodermis, 2–4 layers of small, thick-walled subepidermal cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong, hyaline; rhizoids on primary stems and secondary stems, from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves closely spaced, monomorphic, erect to erect-spreading when wet, erect-spreading, flexuose to somewhat crispate when dry, lanceolate to ovate-lanceolate, 1.2–1.8 mm long, symmetric, concave, abruptly contracted to long, slender acumina; margins entire, plane or erect to broadly infolded above and narrowly recurved below, elimbate; costae double, weak, 1/3–2/3 the leaf length, diverging throughout, smooth at back, not projecting at the apices; cells smooth, median cells linear-fusiform to long-fusiform, 44–100 × 4–10 μm, firm-walled, not porose, lower cells elongate-rectangular, thin-walled, not porose, cells across the base enlarged, subrectangular, often porose, alar region with 2–4 enlarged, quadrate cells or not differentiated. Asexual propagula fusiform, multicellular, uniseriate, arising in terminal clusters on specialized brood branches. Dioicous (?). Sporophytes unknown.

Illustration. Figure 209.
Habitat. On rotting logs; 350 m.
Distribution in Central America. PANAMA. Veraguas: *Crosby 10137* (MO, PMA).
World range: Central America.

Stenodictyon crosbyi is a medium-sized species with glossy, yellowish or reddish green plants and evenly foliate stems. It has concave, lanceolate to ovate-lanceolate leaves that are abruptly contracted above into long, slender acumina. The leaves have firm-walled, elongate-flexuose median leaf cells; short, faint costae that end at or above midleaf; and entire, narrowly recurved margins along most or the entire length of the leaf. The outstanding feature of *S. crosbyi* is the presence of specialized brood branches with propagula borne in dense terminal clusters. Asexual propagula are otherwise absent in *Stenodictyon*, with the exception of a single collection of *S. wrightii* (*Crosby 4394*, MO). In that collection the propagula are borne in clusters abaxial to the leaf insertions opposite the costae. The leaves of *Stenodictyon wrightii* and *S. crosbyi* are very similar in form; those of *S. crosbyi* appear to differ only in having narrowly recurved rather than consistently plane or erect margins.

Asexual propagula are commonly encountered in *Lepidopilum*. That genus also has some species with evenly foliate stems, narrowly acuminate, lanceolate to ovate-lanceolate leaves, and a well-developed stem hyalodermis. There are also some species of *Lepidopilum* with attenuate branch and stem tips, and these sometimes have clusters of gemmae borne abaxially to the leaf insertions. There is, however, no *Lepidopilum* species with specialized brood branches, clusters of terminal gemmae, and lanceolate to ovate-lanceolate leaves abruptly contracted above into long, slender acumina. The two genera differ fundamentally in peristome form: hookeriaceous (*Stenodictyon*) vs. daltoniaceous

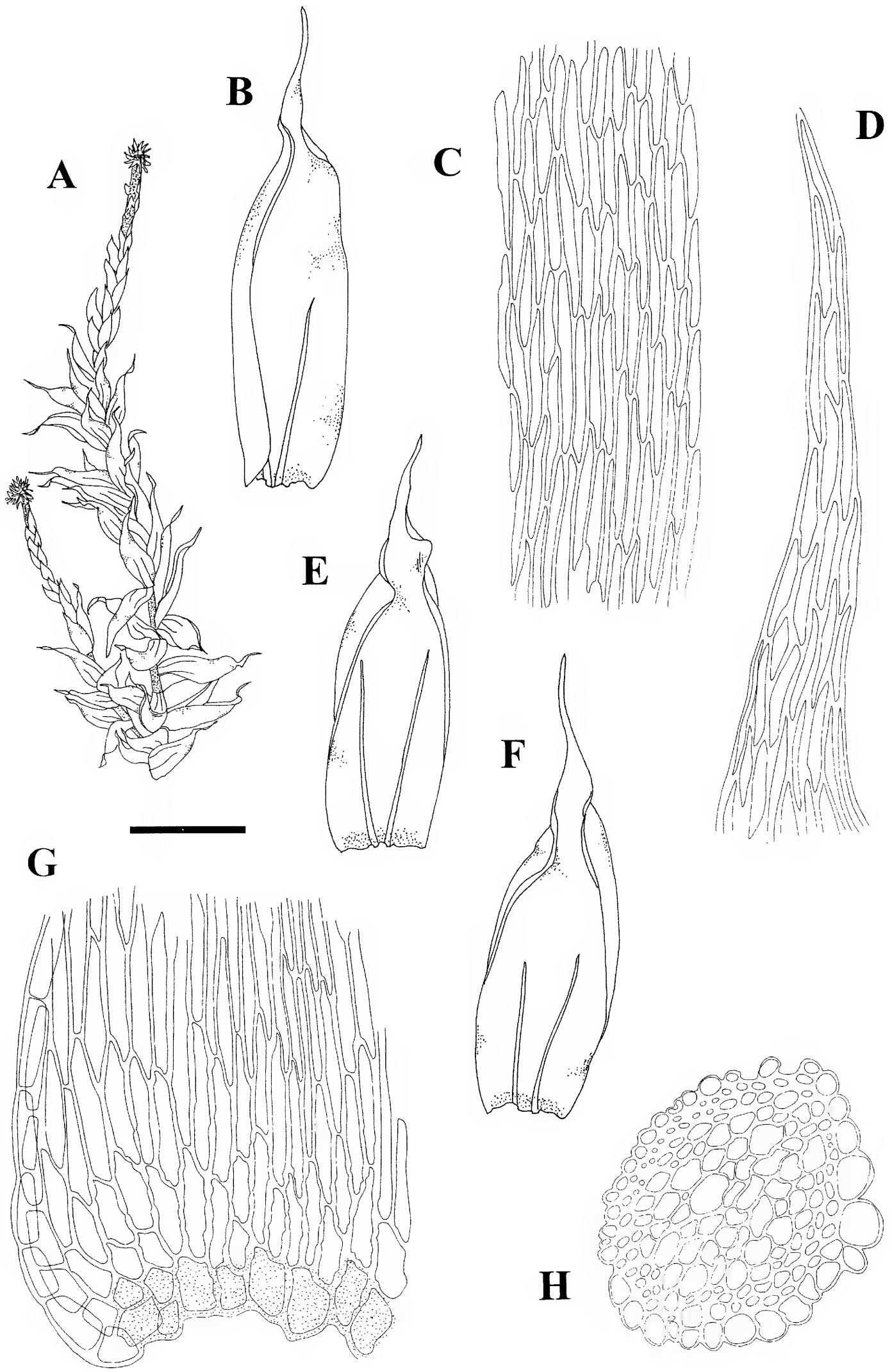
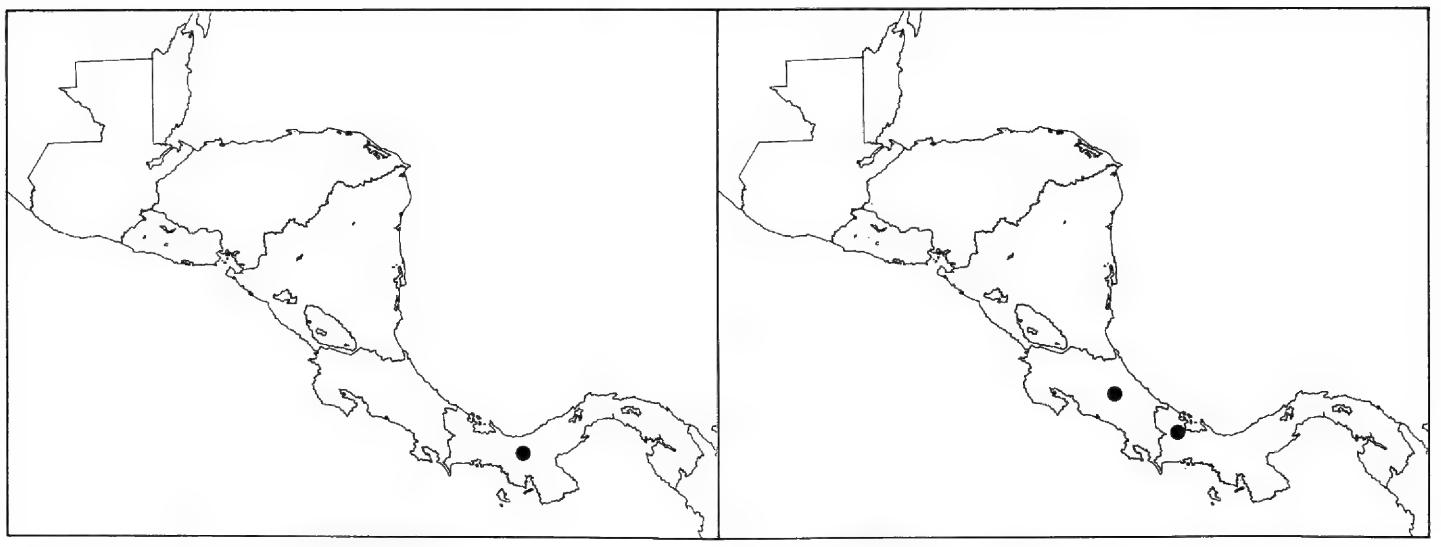


Figure 209. *Stenodictyon crosbyi*. A. Habit. B, E & F. Leaves. C. Median leaf cells. D. Leaf apex. G. Basal and alar cells. H. Stem in cross section. Scale in mm: bar = 0.06 (C, D, G); bar = 0.13 (H); bar = 0.4 (B, E, F); bar = 1.56 (A). All figure parts from *Crosby 10137* (type).



Stenodictyon crosbyi *Stenodictyon ovatum*

(*Lepidopilum*). Whether *S. crosbyi* actually belongs in *Lepidopilum* or *Stenodictyon* cannot be determined for certain until its peristome is discovered.

2. *Stenodictyon ovatum* B. H. Allen, *sp. nov*. Type. Panama. Bocas del Toro: along trail from near Boquete to Cerro Pate Macho and into Bocas, 08°49′N, 082°24′W, *McPherson & Merello 8314F* (MO, holotype).

Species haec a *S. wrightii* foliis longioribus et latioribus ovatis differt.

Plants medium-sized, 2–4 cm long, green, yellowish, or yellow red, in mats. Stems prostrate, irregularly branched, hyaline to yellowish when young, becoming reddish with age, evenly foliate; stems in cross section with well-developed hyalodermis, subepidermal layer of 2–3 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia small, foliose; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect to erect-patent, flexuose-contorted when dry, erect-spreading when wet, monomorphic, ovate to oval, 2.0–2.5 × 0.7–1.0 mm, symmetric, abruptly constricted above to long, slender acumina, concave; margins entire throughout or obscurely sinuate on the acumina, plane to erect, not bordered; costae double, thin, ending 1/3–2/3 the leaf length, diverging throughout, usually unequal, smooth at back, not projecting at the apices; cells smooth, upper cells linear-elongate, 45–100 × 4–6 μm, firm-walled, porose, lower cells oblong-rectangular to long-rectangular, porose, bulging near insertions, cells across the insertions reddish, short-rectangular, porose; alar cells not differentiated. Dioicous. Setae elongate, 25–30 mm long, red, smooth throughout, at times somewhat roughened below the capsules. Capsules horizontal to suberect, oblong-cylindric, 1.5–2.0 mm long, neck well developed; exothecial cells quadrate in 2–4 rows at mouth, those below oblong to rectangular, lateral walls evenly thickened, horizontal walls collenchymatous; stomata rudimentary, 3–4-celled, on neck; operculum and annulus not seen; peristome diplolepideous, exostome narrowly triangular with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface dark red, densely and closely cross-striate below, coarsely papillose above, primary walls yellow, smooth, ventral (inner) surface hyaline to yellowish, deposition thin, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not or faintly perforate, cilia absent. Spores rounded, 12–20 μm, smooth to faintly papillose. Calyptra not seen.

Illustration. Figure 210.
Habitat. On ground in forested slopes; 1500–2200 m.

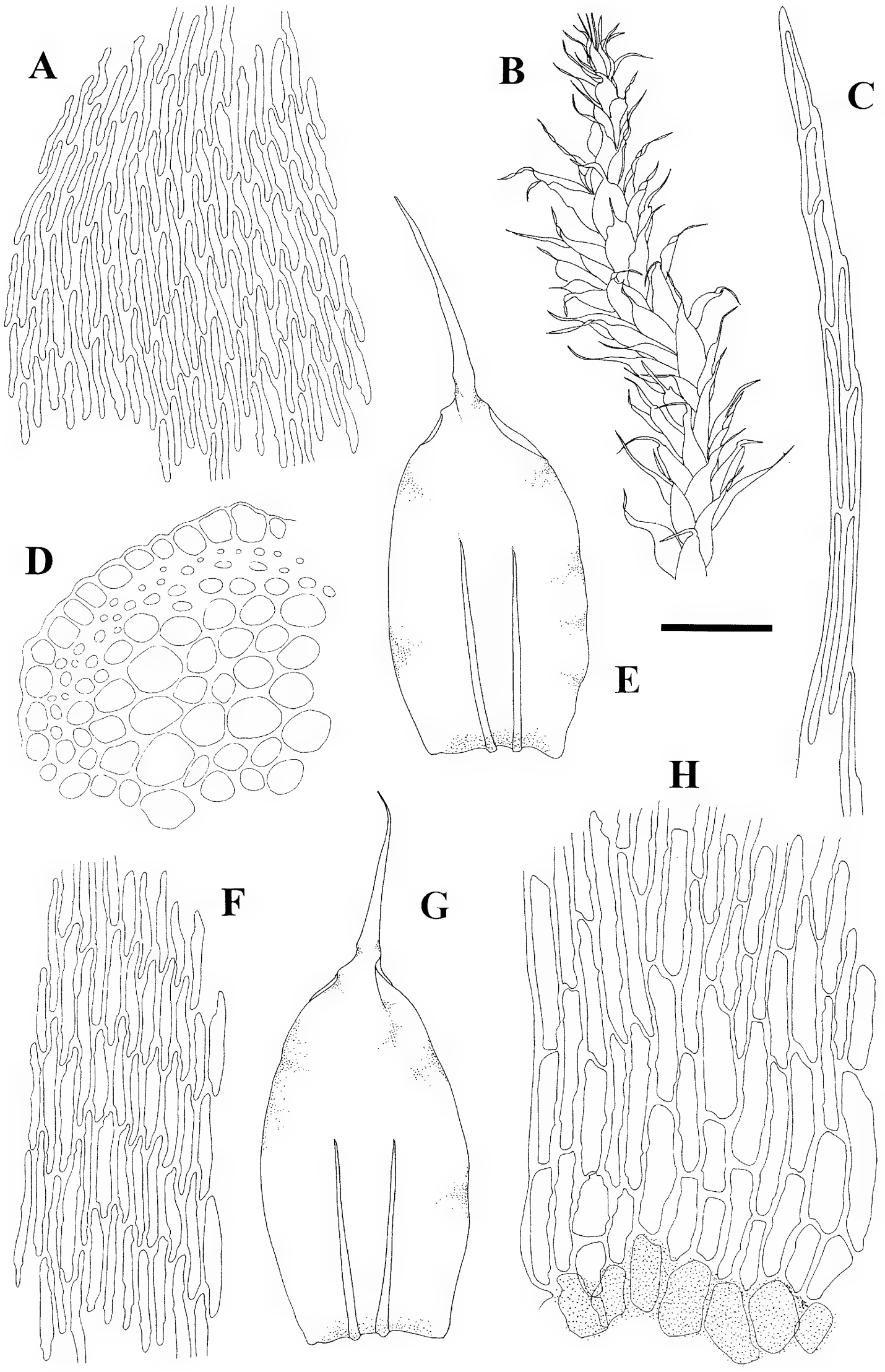


Figure 210. *Stenodictyon ovatum*. A. Upper leaf cells. B. Habit. C. Leaf apex. D. Stem in cross section. E & G. Leaves. F. Median leaf cells between the costae. H. Basal and alar cells. Scale in mm: bar = 0.06 (A, F, H); bar = 0.07 (C); bar = 0.13 (D); bar = 0.5 (E, G); bar = 2.0 (B). All figure parts from *McPherson & Merello 8314F* (type).

Distribution in Central America. COSTA RICA. Cartago: *Buck 44141* (MO, NY). PANAMA. Bocas del Toro: *McPherson & Merello 8314F* (MO).

World range: Central America.

Stenodictyon ovatum is a medium-sized species with evenly foliate leaves that are erect-patent and somewhat glossy when dry. It has an exceptionally well-developed stem hyalodermis and broad, ovate to oval leaves that are abruptly constricted at the base into long, slender acumina. The upper leaf margins in *Stenodictyon ovatum* are mostly entire throughout, but the margins of the acumina are sometimes obscurely sinuate. Its upper and median leaf cells are firm- to thick-walled, porose, and narrowly linear except at the base, where they become enlarged and variously rectangular.

Stenodictyon wrightii and *S. pallidum* differ from *S. ovatum* in having smaller, narrower, oblong-lanceolate leaves. In most gametophytic and sporophytic features *S. ovatum* is identical to *Thamniopsis steyermarkii*. This species differs from *S. ovatum* in having strongly to moderately serrate upper leaf margins.

3. *Stenodictyon pallidum* E. Britton *ex* H. A. Crum & Steere, Bryologist 59: 252. 1957. Protologue. Puerto Rico: On rotten log, high ridge, road between Maricao and Sabana Grande, at km. 15, Maricao Insular Forest, *W. C. Steere 5782*. Type. Puerto Rico. On rotten log, high ridge, km. 15, road from Maricao to Sabana Grande, Maricao Insular Forest, Dec. 31, 1939, *William Campbell Steere 5732* [sic] (MO, isotype).

Plants small to medium-sized, 1–2 cm long, pale green, reddish yellow, or yellowish, in mats. Stems prostrate, irregularly branched, hyaline to yellowish when young, becoming reddish with age, evenly foliate; stems in cross section with hyalodermis, subepidermal sclerodermis sometimes present, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia small, foliose; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect to erect-spreading, at times lightly undulate when dry, erect-spreading when wet, monomorphic, oblong-lanceolate, 1.0–1.6 × 0.2–0.4 mm, symmetric, abruptly constricted above to piliferous acumina, concave; margins entire throughout or subentire in upper 1/4, plane to erect, not bordered; costae double, thin, ending 1/3 the leaf length, diverging throughout, usually unequal, smooth at back, not projecting at the apex; cells smooth, upper cells long-rhomboidal, 24–100 × 6–14 µm, thin-walled, lower cells oblong-rectangular to long-rectangular, bulging near insertions, cells across the insertions short-rectangular; alar cells not differentiated. Autoicous. Setae elongate, 8–15 mm long, red, smooth throughout. Capsules horizontal to pendent, oblong-cylindric, 0.7–1.0 mm long, neck well developed; exothecial cells reddish, quadrate in 2–4 rows at mouth, those below oval to oblong, collenchymatous; stomata rudimentary, 3–5-celled, on neck; opercula conic-rostrate, 0.7 mm long; annuli of 3–5 rows of yellowish, thin-walled cells, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome narrowly triangular with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface dark red, densely and closely cross-striate below, coarsely papillose above, primary walls yellow, smooth, ventral (inner) surface hyaline to yellowish, deposition thin, lightly papillose; endostome as long as the exostome, yellow, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not or faintly perforate, cilia absent. Spores rounded, 8–12 µm, papillose. Calyptrae mitrate, 1.5–2.0 mm long, yellowish, irregularly lobed at base, naked or sparsely hairy.

Illustrations. Crum and Steere (1957, Fig. 43); Welch (1969, Figs. 222–229); Duarte Bello (1997, Pl. 255); Buck (1998, Pl. 18 6–13). Figure 211.

Habitat. On rotting logs and soil; 500–1500 m.

Not known from Central America.

World range: Caribbean.

Stenodictyon pallidum is a small to medium-sized, pale green to yellowish species with evenly foliate leaves that are erect to erect-spreading when dry. Its oblong-lanceolate leaves are abruptly con-

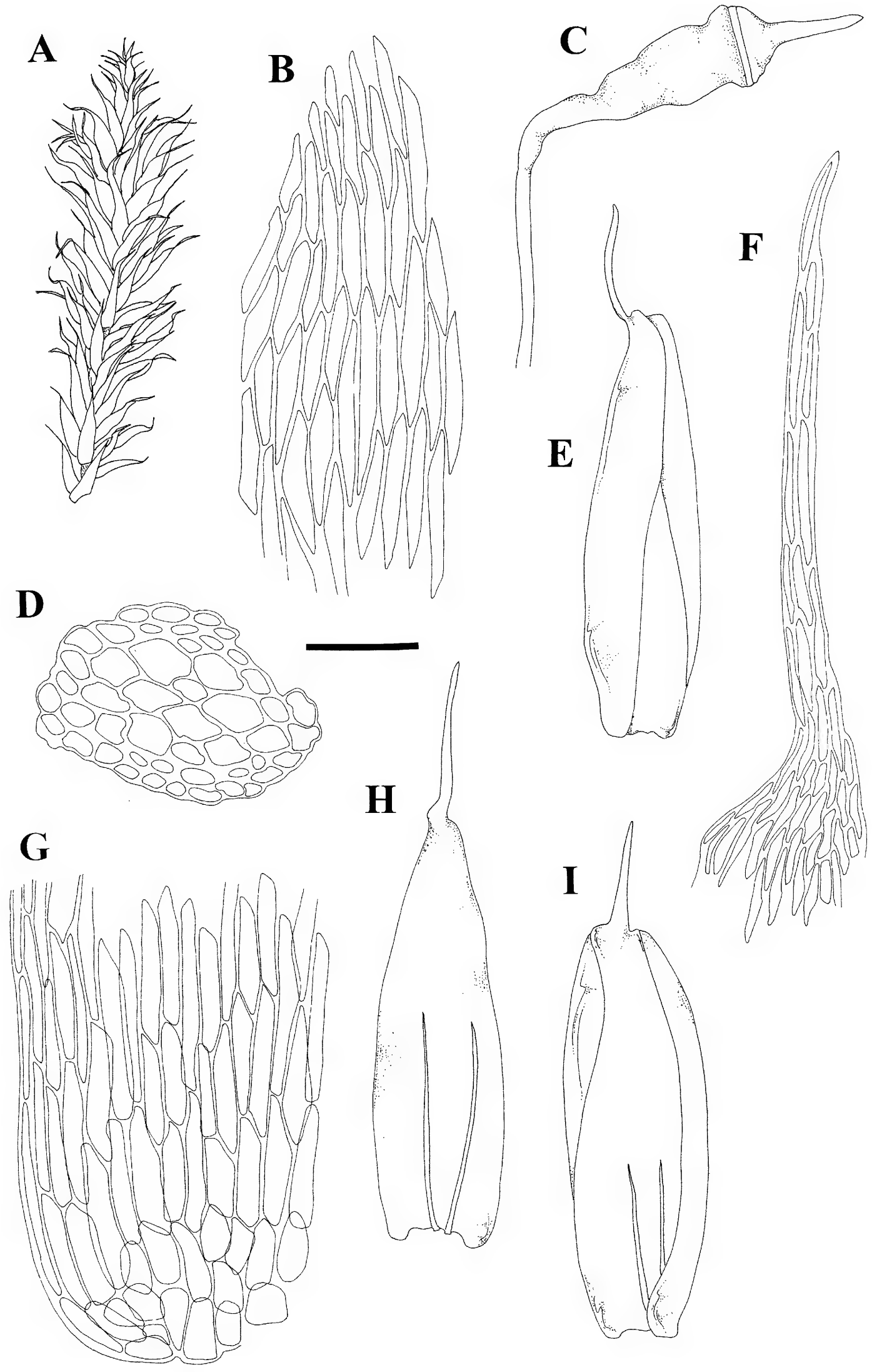


Figure 211. *Stenodictyon pallidum*. A. Habit. B. Upper leaf cells. C. Seta, capsule, annulus, and operculum. D. Stem in cross section. E, H & I. Leaves. F. Leaf apex. G. Basal and alar cells. Scale in mm: bar = 0.06 (B, D, F, G); bar = 0.28 (E, H, I); bar = 0.5 (C); bar = 1.3 (A). B, F, G from *Pagan 304*; C from *Steere 5520*; all other figure parts from *Steere 5782* (type).

stricted at the base to long, slender, acumina. The upper leaf margins in *S. pallidum*, while mostly entire, are at times subentire above. Its long-rhomboidal upper leaf cells are smooth, relatively broad, and have lax, bulging walls. Although the upper leaf cells are remarkably variable in length and width, it is always possible to find some cells over 10 µm wide. Its costae are thin, smooth at back, do not project at the tips, and end about midleaf. *Stenodictyon pallidum* has fairly short setae, long-rostrate opercula, and short capsules with distinctly collenchymatous exothecial cells. An outstanding feature of the *S. pallidum* sporophyte is the presence of a massive annulus consisting of thin-walled, yellowish cells that are persistent at the base of the operculum. This annulus is identical in form to the massive annuli found in many species of *Thamniopsis*.

Stenodictyon wrightii is nearly identical to *S. pallidum* in plant size and aspect. The leaves in both species are oblong-lanceolate, with thin, smooth costae, entire margins, and smooth cells. *Stenodictyon wrightii* differs from *S. pallidum* in having longer setae (35–50 mm), longer capsules (2–3 mm), and narrow (3–6 µm), firm-walled, linear or elongate-rectangular upper leaf cells that are often sigmoid shaped.

The collection numbers on the holotype (MICH) and one isotype (MO) do not agree with the collection number in the protologue. This discrepancy is the result of a transcriptional error made in typing the original labels (see Allen *et al.* 1986).

4. *Stenodictyon wrightii* (Sull. & Lesq.) Crosby, Bryologist 79: 83. 1976. *Hookeria wrightii* Sull. & Lesq., Proc. Amer. Acad. Arts 4: 282. 1859. *Hypnella wrightii* (Sull. & Lesq.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 366. 1877. Protologue. [Nicaragua] [On bushes, summit of a mountain on the Island of Ometepe, in Lake Nicaragua], growing with *Hypnum Ometepense* [*Charles Wright*] *33*. Types. Ometepe summit on bushes in shade, Nicaragua, *Wright* (FH, holotype; NY, isotype).

Hookeria nitida Mitt., J. Linn. Soc., Bot. 12: 348. 1869. *Stenodictyon nitidum* (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 358. 1877. Protologue. [Ecuador] Andes Quitenses, in monte Tunguragua, loco Mapa-yacu, ad terram (10,000 ped.), *Spruce, n. 707*. Types. Andes Quitenses, Tunguragua, Mapa-yacu ad tam, 10,000 ped., *Spruce 707* (NY, holotype; BM, FH, MICH, isotypes).

Stenodictyon sericeum E. B. Bartram, J. Wash. Acad. Sci. 19: 23. 1929. Protologue. La Palma, Costa Rica, altitude 1,500 meters, April 30, 1928, *Valerio 146*. Types. Plants of Costa Rica. La Palma, 1500 m. Apr. 30–1928, *Manuel Valerio 146* (US, holotype; FH, MICH, NY, isotypes).

Plants small to medium-sized, 2–4 cm long, green, reddish, yellowish, or yellow brown, in mats. Stems prostrate, irregularly to subpinnately branched, hyaline to yellowish when young, becoming reddish with age, evenly foliate; stems in cross section with hyalodermis, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia small, foliose; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect to erect-spreading, at times lightly undulate when dry, erect-spreading when wet, monomorphic, oblong-lanceolate, 1.2–2.0 × 0.3–0.5 mm, symmetric, abruptly constricted above to piliferous acumina, concave; margins entire throughout or subentire in upper 1/4, plane to erect, not bordered; costae double, thin, ending 2/3 the leaf length, diverging throughout, usually unequal, smooth at back, not projecting at the apices; cells smooth, upper cells linear-elongate, sinuate, 40–80 × 3–6 µm, firm-walled, at times porose, lower cells oblong-rectangular to long-rectangular, bulging near insertions, cells across the insertions short-rectangular, reddish; alar cells not differentiated. Asexual propagula fusiform, multicellular, uniseriate, arising abaxial to the leaf insertions opposite the costae on specialized brood branches. Autoicous or paroicous. Setae elongate, 35–50 mm long, red, smooth throughout, at times somewhat roughened below the capsules. Capsules horizontal to pendent, oblong-cylindric, 2–3 mm long, neck well developed; exothecial cells reddish, quadrate in 2–4 rows at mouth, those below oblong to rectangular, walls evenly thickened to slightly collenchymatous; stomata rudimentary, 3–5-celled, on neck; operculum and annulus not seen; peristome diplolepideous, exostome narrowly triangular with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface dark red, densely and closely cross-striate below, coarsely papillose above, primary walls yellow, smooth, ventral (inner) surface hyaline to yellowish, deposition thin, lightly papillose; endostome as long as the exostome, yellowish, lightly

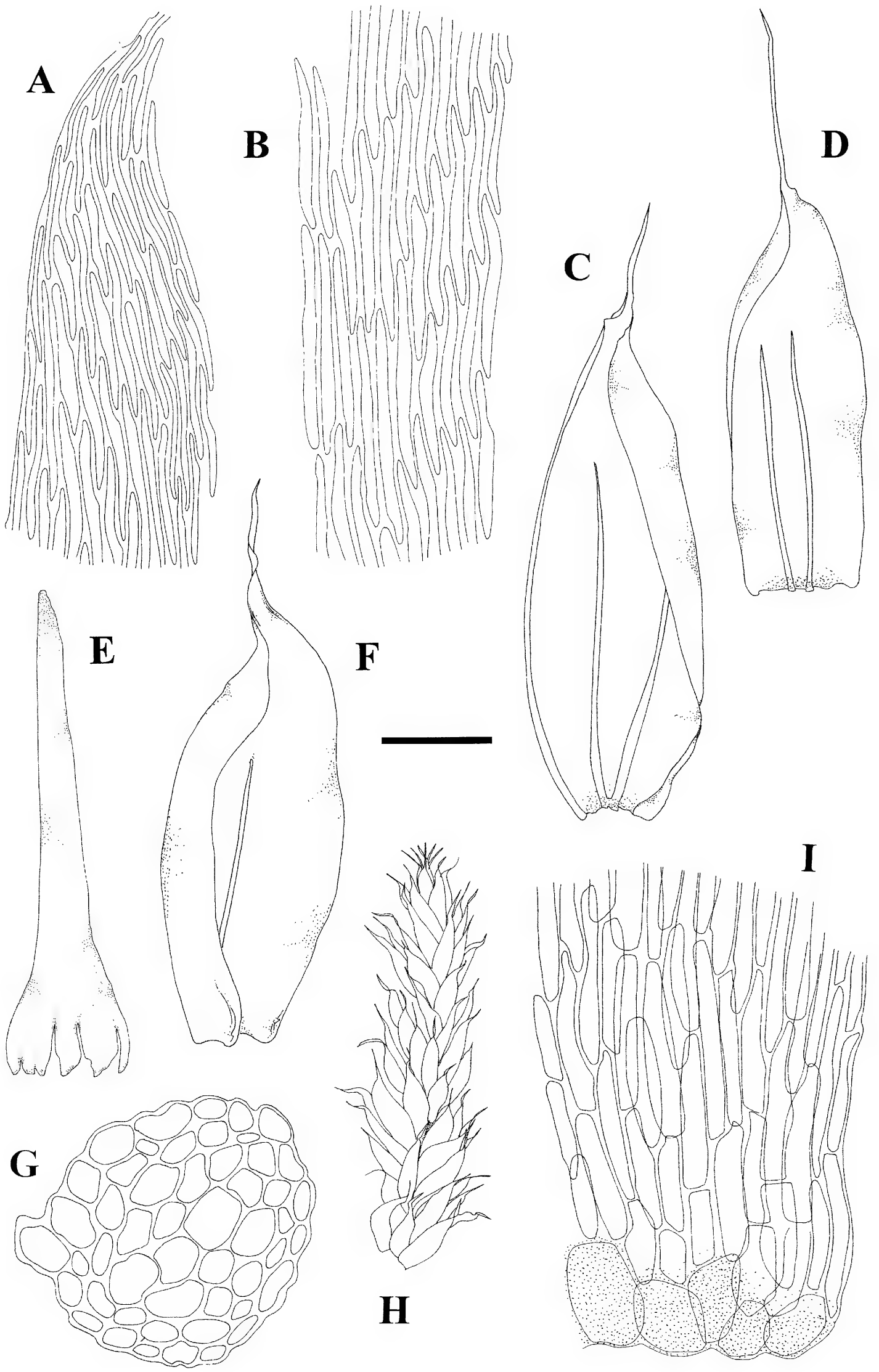
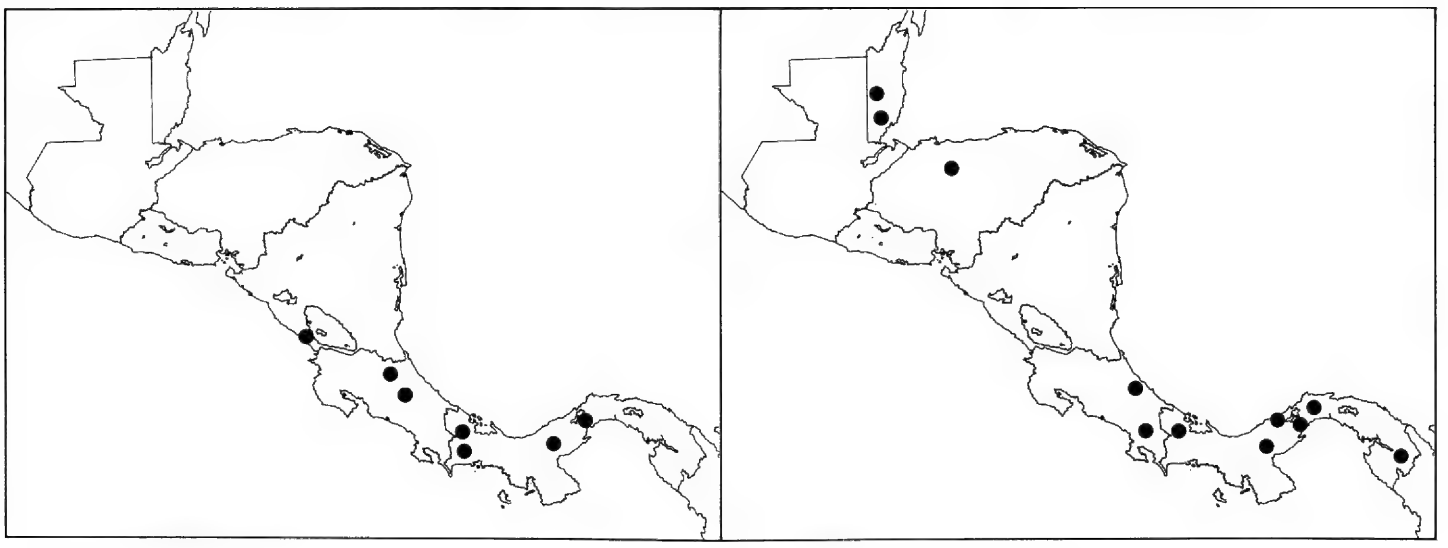


Figure 212. *Stenodictyon wrightii*. A. Upper leaf cells and margin. B. Median leaf cells. C, D & F. Leaves. E. Calyptra. G. Stem in cross section. H. Habit. I. Basal and alar cells. Scale in mm: bar = 0.06 (A, B, G, I); bar = 0.28 (C, D, F); bar = 0.6 (E); bar = 1.96 (H). D from *Valerio 146* (type *S. sericeum*); E from *Crosby & Crosby 6594*; F from *Wright* (type); all other figure parts from *Crosby & Crosby 5948*.



Stenodictyon wrightii *Thamniopsis colombica*

papillose throughout, basal membranes high, segments broad, strongly keeled, not or faintly perforate, cilia absent. Spores rounded, 26–32 µm, papillose. Calyptrae mitrate, 3.0 mm long, reddish yellow, irregularly lobed at base.

Illustrations. Bartram (1929, Fig. 1 L–R); Welch (1974, Figs. 269–272, 432–453); Churchill and Linares (1995, Fig. 44 a–f); Gradstein *et al.* (2001, Fig. 169 J–O). Figure 212.

Habitat. On tree trunks, branches, twigs, rotting logs, wood, and humus; 732–2680 m.

Distribution in Central America. NICARAGUA. Rivas: *Wright 33* (FH, NY). COSTA RICA. Cartago: *Crosby & Crosby 5948* (CR, MO); Heredia: *Crosby & Crosby 6594* (MO). PANAMA. Bocas del Toro: *Allen 5772* (MO); Canal Area: *Lewis et al. 4653A* (MO); Chiriquí: *Crosby 4010* (MO); Coclé: *Crosby 4394* (MO).

World range: Central America; Western South America.

Stenodictyon wrightii is a small to medium-sized species with evenly foliate leaves that are erect to erect-spreading and occasionally undulate when dry. Its oblong-lanceolate leaves are abruptly constricted at the base of long, slender acumina. The leaves have typically entire upper margins or occasionally the margins of acumina can be subentire; long, narrowly linear and usually sinuose leaf cells; enlarged, variously rectangular, often light reddish basal cells across the insertions; and thin, smooth costae that end in the upper parts of the leaves and do not project at the tips. The setae of *S. wrightii* are remarkably long, and at times they reach 50 mm in length.

Stenodictyon pallidum is similar to *S. wrightii* in overall size and aspect. Both species also have similarly shaped leaves. The former differs from *S. wrightii* in having shorter setae (8–15 mm) and thin-walled, long-rhomboidal upper leaf cells. *Stenodictyon ovatum* is a larger species than *S. wrightii*, and it has considerably larger, broader leaves. The presence of monomorphic leaves that are constricted at the base of the acumina is a feature also found in *Thamniopsis steyermarkii*, the *acicularis*-form of *T. undata*, *T. glandulifera*, and *T. purpureophylla.* These species differ from *S. wrightii* in having sharply serrate leaf margins. The *acicularis*-form of *T. undata* further differs from *S. wrightii* in having strongly undulate leaves with broader upper leaf cells (3–14 µm vs. 3–6 µm). Additionally, *Thamniopsis purpureophylla* differs in having a reddish purple color and distinctly prorate upper leaf cells, while *T. glandulifera* has leaf cells with high, spiculose papillae.

Excluded taxa

Stenodictyon bisodalense B. H. Allen, Crosby & Magill, Lindbergia 11: 155. 1986. Protologue. Costa Rica. Dos Amigos area, near 73 km marker on Inter American Highway, SE of El Empalme. *Sphagnum-Blechnum* bog, 2680 m, 9°37′N, 83°50′W, *Crosby & Crosby 5956*. Type. Costa Rica. Cartago: Dos Amigos area, near 73 km marker on Inter American Highway, SE of El Empalme.

Sphagnum-Blechnum bog. 2680 m altitude. 9°37′N, 83°50′W, 26.iii.1973, *Marshall R. & Carol A. Crosby 5956* (MO, holotype).

As noted by Churchill and Linares (1995) this species is a synonym of *Lepidopilum longifolium* Hampe.

16. *Thamniopsis* (Mitt.) M. Fleisch., Musci Buitenzorg 3: 952. 1908. *Hookeria* Sm. sect. *Callicostella* Müll. Hal. subsect. *Thamniopsis* Mitt., J. Linn. Soc., Bot. 12: 338. 1869. *Hookeriopsis* (Besch.) A. Jaeger sect. *Thamniopsis* (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 364. 1877.

Hookeriopsis (Besch.) A. Jaeger sect. *Pseudo-Omaliadelphus* Broth., Nat. Pflanzenfam. I(3): 942. 1905.

Plants small, medium-sized, or robust, pale greenish, green, or yellowish red, in dense or loose mats. Stems prostrate, irregularly to irregularly pinnately branched, at times becoming subdendroid, hyaline to yellowish when young, becoming reddish with age; stems in cross section with hyalodermis, subepidermis of 2–3 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent, rarely filamentous or foliose, foliose scale leaves present; axillary hairs 2-celled; rhizoids from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves monomorphic or dimorphic, smooth or undulate, ovate, obovate, oblong-ovate, oblong-ligulate, oblong-lanceolate, or lanceolate, symmetric or asymmetric, rounded to obtuse, gradually acute to short-acuminate; margins entire, serrate, or dentate in upper 2/3, teeth at times swollen, often bifid, entire below, plane to erect, at times broadly incurved on one side at base, marginal cells at times forming a border; costae double, ending 2/3–3/4 the leaf length, diverging throughout, unequal, serrate or smooth on back, often projecting at the apices; cells smooth, upper cells isodiametric, hexagonal, short-oblong, long-rhomboidal, elongate-flexuose, or linear-flexuose, thin- or thick-walled, porose or eporose, lower cells elongate-rhomboidal, to long-rectangular; basal cells near the insertions enlarged, oblong-rectangular; alar cells not differentiated. Dioicous, autoicous, or synoicous. Setae elongate, flexuose, smooth, at times roughened on neck or scabrose throughout. Capsules horizontal to erect, ovoid, short-cylindric, or oblong-cylindric, neck well developed; exothecial cells variously collenchymatous; stomata rudimentary, on neck; opercula conic-rostrate; annuli usually of 7–9 (occasionally to 20) rows of cells, separating from capsule along dehiscent zone at base and persistent on the operculum, rarely of 2–3 rows of thin-walled cells; peristome diplolepideous, exostome narrowly triangular with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface dark red, densely and closely cross-striate below, coarsely papillose above, primary walls yellow, smooth, ventral (inner) surface hyaline to yellowish, deposition thin, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not or faintly perforate, cilia absent. Calyptrae mitrate, irregularly lobed or laciniate-fringed at base, naked or sparsely hairy.

The genus *Thamniopsis* occurs in tropical and south temperate regions of the New World and Africa. Fleischer (1908) established the genus for a single Ecuadorian species that had a subdendroid, thamnioid-like habit, evenly foliate stems, obtuse leaves, and the long-necked capsules of *Hookeriopsis*. Bartram (1928a) added a second species to *Thamniopsis*. Buck (1987) considerably expanded the generic concept of *Thamniopsis* when he transferred 13 species of *Hookeriopsis* into the genus. There are now 18 species in the genus, but more will likely be moved into *Thamniopsis* from *Hookeriopsis* after the latter genus is thoroughly revised. Plants of *Thamniopsis* are often robust in size, and they can be dark green, green, yellowish green, or reddish in color. Its stems have a distinct hyalodermis and pseudoparaphyllia are usually absent. An outstanding feature of *Thamniopsis* is the astounding degree of leaf polymorphism found in some species. The leaves from a single stem are often radically different, and the transition from one form to another is often abrupt, *i.e.*, occurring within the space of 2–4 leaves. The leaves from a single plant of *Thamniopsis* can be undulate to rugose or smooth when dry, oblong or lanceolate, and long-acuminate or obtuse. The leaf margins can vary from serrate to dentate with short, swollen, bifid teeth; serrate to subentire with sharp, non-

swollen teeth that are never bifid; or entire. The leaves can be distinctly bordered to weakly bordered by elongate cells or elimbate. The costae in *Thamniopsis* end above midleaf and diverge throughout. Some leaves usually have costae that are serrate at back and project at the tips, but in others the costae are smooth at back and do not project at the tips. The leaves of *Thamniopsis* typically have a heterogeneous areolation in which the upper and median cells are firm- or thick-walled and the basal cells are enlarged, bulging, and thin-walled. The capsules of *Thamniopsis* are distinctive in having a massive, persistent annulus consisting of 7–9 rows of yellowish, hexagonal cells. As in other members of the Hookeriaceae, the rudimentary stomata are made up of 2–6 cells. *Thamniopsis* has a typical hookeriaceous peristome. The calyptrae are mitrate, irregularly fringed at base, and sometimes sparsely hairy.

In Central America *Thamniopsis* can be confused with *Hookeriopsis*, *Brymela*, or *Trachyxiphium.* All three genera differ from *Thamniopsis* in having a sclerodermis rather than a hyalodermis on the outside layer of the stems. *Hookeriopsis* further differs from *Thamniopsis* in having leaves with short double costae (ending below midleaf) and a homogeneous areolation of long, narrow, firm-walled cells. Some *Brymela* species are nearly identical to *Thamniopsis* in size and aspect, and both genera have species with undulate or rugose leaves. *Brymela* differs from most species of *Thamniopsis* in having weakly toothed leaf margins with teeth that are never swollen or bifid. In addition, the leaf cells in *Brymela* are similar to those of *Hookeriopsis* in being homogeneous throughout (consisting of elongate, firm- to thick-walled cells), and typically the genus has smooth costae that only weakly project at the tips. *Trachyxiphium* and *Thamniopsis* are similar in having thin-walled leaf cells, leaf margins with swollen, often bifid teeth, and strong costae that are spined or crested with paired, bifid teeth. The former differs from *Thamniopsis* in having leaf cells that are homogeneous throughout and often prorate.

As presently circumscribed *Stenodictyon* is not distinct from *Thamniopsis*. Furthermore, *Stenodictyon* is the older name, and combining the two genera would require a large number of nomenclatural transfers. As presently circumscribed *Thamniopsis* is a large, variable genus that may be polyphyletic. In order to clarify its generic boundaries not only is it in need of revision, but the genus *Hookeriopsis sensu* Brotherus (1925) should also be revised. In the interest of nomenclatural stability it seems best to refrain from making wholesale transfers of *Thamniopsis* species into *Stenodictyon* until *Thamniopsis* and *Hookeriopsis* have been critically revised.

The name *Thamniopsis* combines the generic name *Thamnium* with the Greek *opsis* (aspect or appearance).

1. All leaves with rounded apices and entire margins . . . . . 8. *T. pendula*
1. Some or all leaves with acuminate to subulate or truncate apices and serrulate, serrate, or dentate margins 2

2. Upper leaf margins with short, massive, greatly swollen, bifid teeth 3
2. Upper leaf margins entire to dentate, teeth not or moderately enlarged and bifid 4

3. Leaves ovate to obovate, asymmetric, broadly obtuse; upper leaf cells hexagonal to rhomboidal, 50–90 × 20–26 µm . . . . . 6. *T. incurva*
3. Leaves ovate-lanceolate, symmetric, narrowly acute to acuminate; upper leaf cells linear-flexuose, 90–100 × 6–10 µm . . . . . 7. *T. oedodontia*

4. Plants slender, 1–3 cm long; leaves 0.6–1.5 mm long 5
4. Plants medium-sized to robust, 3–12 cm long; leaves 1.0–4.0 mm long 11

5. Upper cells on dorsal and lateral leaves thin-walled, 10–20 µm wide . . . . . 1. *T. colombica*
5. Upper cells on dorsal and lateral leaves firm-walled, less than 10 µm wide 6

6. Leaves abruptly constricted at base of acumina 7
6. Leaves gradually narrowed to the apex 9

7. Upper leaf cells smooth . . . . . 12. *T. steyermarkii*
7. Upper leaf cells prorate or spiculose-papillose 8

8. Leaves reddish to purple tinged; upper leaf cells prorate . . . . . 9. *T. purpureophylla*
8. Leaves pale to yellow green; upper cells spiculose-papillose . . . . . 4. *T. glandulifera*

9. Leaves undulate, lanceolate to oblong-ovate, long-acuminate; upper margins undulate and irregularly recurved, marginal teeth at times multicellular; upper cells often prorate, 2–4 µm wide; costae dentate to crested at back; calyptrae laciniate-fringed . . . . . 11. *T. standleyi*
9. Leaves smooth, oblong-ovate to oblong-lanceolate, acute to short-acuminate; upper margins plane to erect, marginal teeth unicellular; upper cells smooth, 5–10 µm wide; costae smooth to serrate at back; calyptrae irregularly lobed 10

10. Leaf margins with somewhat swollen, often bifid teeth . . . . . 5. *T. guatemalensis*
10. Leaf margins with non-swollen, single teeth . . . . . 10. *T. rivularis*

11. Leaves monomorphic 12
11. Leaves strongly dimorphic, some leaves with rounded apices and entire margins, other leaves shortly acuminate to truncate with coarsely serrate margins 15

12. Leaves gradually acuminate, strongly undulate . . . . . 13. *T. undata*
12. Leaves constricted at base of acumina or subulae, undulate or smooth 13

13. Leaves strongly undulate, broadly acuminate; upper leaf cells long-hexagonal, 3–14 µm wide, marginal teeth somewhat swollen . . . . . 13. *T. undata* [*acicularis*-form]
13. Leaves smooth or weakly and sporadically undulate, narrowly acuminate to subulate; upper leaf cells linear, 2–4 µm wide, marginal teeth not swollen 14

14. Upper leaf cells smooth . . . . . 12. *T. steyermarkii*
14. Upper leaf cells spiculose-papillose . . . . . 4. *T. glandulifera*

15. Serrate leaves acuminate, acute or truncate with 2–5 rows of rounded to oblate cells at the tips; margins consistently bordered by quadrate to short-rectangular cells, intramarginal borders well developed; cells along the costae enlarged and bulging, distinctly different from median cells; margin consistently serrate to dentate, the teeth often multicellular . . . . . 3. *T. diffusa*
15. Serrate leaves acute to acuminate with a single row of rounded to oblate cells at the tips; margins usually bordered by elongate cells, intramarginal borders weakly developed or absent; cells along the costae similar to median cells; marginal teeth almost always unicellular . . . . . 2. *T. cruegeriana*

1. *Thamniopsis colombica* (R. S. Williams) B. H. Allen, *comb. nov.* Basionym: *Callicostella colombica* R. S. Williams, Bryologist 28: 61. 1925. *Schizomitrium colombicum* (R. S. Williams) W. R. Buck & Steere, Moscosoa 2: 47. 1983. *Schizomitrium colombicum* (R. S. Williams) H. A. Crum, Bryologist 87: 208. 1984, superfluous combination. Protologue. Cordoba, Department of El Valle, Colombia. *E. P. Killip*, May 6–8, 1922, *5044*. Types. Department of El Valle, Cordoba, Dagua Valley. Wooded cliff of Rio Dagua, alt. 80–100 m, *Ellsworth P. Killip No 5044* May 6, 8, 1922 (FH, US, isotypes).

Callicostella grossiretis E. B. Bartram *in* B. Willis, Bryologist 42: 156. 1939. *Schizomitrium grossirete* (E. B. Bartram *in* B. Willis) H. A. Crum, Bryologist 87: 208. 1984. *Schizomitrium grossirete* [*is*] (E. B. Bartram *in* B. Willis) J. Florsch., Fl. Suriname 6(1, II): 324. 1986, superfluous combination. Protologue. [Panama] Barro Colorado Island, Canal Zone, *B. Willis*. Types. Panama Canal Zone, Barro Colorado Island, on fallen log, along brook, on Standley trail, 29 Jan. 1938, *Barbara Willis 41* (FH, holotype; F, US, isotypes).

Callicostella tenerrima E. B. Bartram, Bryologist 54: 238. 1951. *Schizomitrium tenerrimum* (E. B. Bartram) H. A. Crum, Bryologist 87: 208. 1984. Protologue. [Costa Rica] Prov. Cartago: Turrialba, Institute of Inter-American Agricultural Sciences, immediate vicinity, elev. about 1872 ft., *Ruth D. Svihla 3004*, Oct. 12–24, 1947. Type. Costa Rica: Prov. Cartago: Institute of Inter-American Agricultural Sciences, immediate vicinity: Atlantic slope: elev. about 1872 ft., *Ruth D. Svihla.* Oct. 12–24, 1947. *No. 3004* (FH, holotype), *syn. nov.*

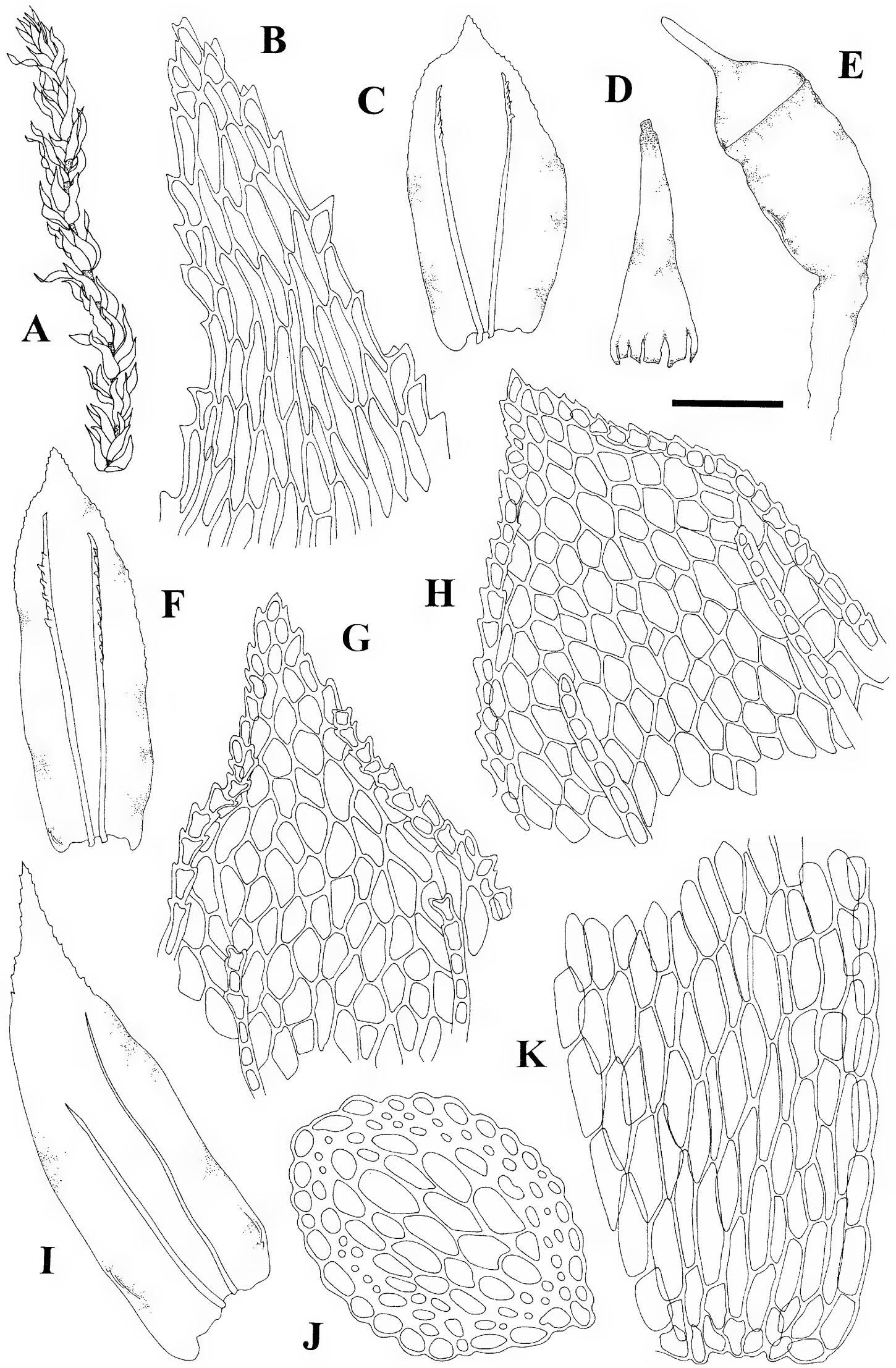


Figure 213. *Thamniopsis colombica*. A. Habit. B. Leaf apex, ventral leaf. C & F. Lateral leaves. D. Operculum. E. Seta, capsule, and operculum. G & H. Leaf apices. I. Ventral leaf. J. Stem in cross section. K. Basal and alar cells. Scale in mm: bar = 0.06 (B, G, H, J, K); bar = 0.26 (C, F, I); bar = 0.36 (D, E); bar = 1.56 (A). C, H, J, K from *Willis* (type *Callicostella grossiretis*); D, E from *Meyer 65*; F, G from *Killip 5044* (type); all other figure parts from *Allen 18726*.

Plants small and slender, 1–3 cm long, pale greenish, green, or yellowish red, in dense or loose mats. Stems prostrate, irregularly branched, hyaline to yellowish when young, becoming reddish with age; stems in cross section with moderate-sized hyalodermis, subepidermis of 2–3 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent, foliose scale leaves present; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect-flexuose when dry, erect-spreading when wet; dorsal and lateral leaves oblong-lanceolate to lanceolate, 0.6–1.2 mm long, symmetric, gradually acute to short-acuminate; margins serrate to dentate in upper 2/3, teeth slightly swollen, often bifid, entire below, plane to erect; costae double, ending 2/3–3/4 the leaf length, diverging throughout, unequal, serrate on back, projecting at the apices by one or more swollen cells; cells smooth, upper cells variable, isodiametric, hexagonal to long-rhomboidal, 18–36 × 10–20 µm, thin-walled, eporose, lower cells elongate-rhomboidal to long-rectangular; basal cells near the insertion enlarged, oblong-rectangular; alar cells not differentiated; ventral leaves erect, lanceolate, 0.6–1.0 mm long, symmetric, short-acuminate; margins serrate in upper 2/3, teeth elongate, rarely bifid, entire below; costae double, slender, ending 2/3 the leaf length, diverging throughout, unequal, smooth on back, not projecting at the apex; upper cells elongate-flexuose. Dioicous. Setae elongate, 4–10 mm long, red, flexuose, scabrose in Central America, smooth to somewhat roughened in Colombia. Capsules horizontal to erect, ovoid to short-cylindric, 0.5–1.0 mm long, neck well developed; exothecial cells quadrate to oblate in 2–4 rows at mouth, those below oblong to rectangular, lateral walls evenly thickened, horizontal walls somewhat collenchymatous; stomata rudimentary, on neck; opercula conic-rostrate, 0.5 mm long; annuli of 7–9 rows of cells, lower cells transversely rectangular, upper cells quadrate, all cells thin-walled with irregular nodose thickenings, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome narrowly triangular with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface dark red, densely and closely cross-striate below, coarsely papillose above, primary walls yellow, smooth, ventral (inner) surface hyaline to yellowish, deposition thin, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not or faintly perforate, cilia absent. Spores rounded, 8–10 µm, smooth to faintly roughened. Calyptrae mitrate, 1 mm long, yellowish white, red at times, irregularly lobed at base, smooth.

Illustrations. Willis (1939, Fig. 5 a–d); Welch (1974, Figs. 20–31); Florschütz-de Waard (1986, Fig. 126); Churchill and Linares (1995, Fig. 35 a–e); Buck (1998, Pl. 24 12–18); Buck (2003, Fig. 85). Figure 213.

Habitat. On rotting logs, trees, soil along streams, and on limestone tufa; sea level to 730 m.

Distribution in Central America. BELIZE. Cayo: *Allen 18466* (BRH, MO); Toledo: *Allen 18726* (BRH, MO). HONDURAS. Yoro: *Allen 13628* (MO). COSTA RICA. Limón: *Steere CR-162* (MO, NY); Puntarenas: *Gentry & Burger 2791C* (CR, MO). PANAMA. Bocas del Toro: *Allen 5681C* (MO); Canal Area: *Meyer 71* (NY, US); Coclé: *Hunter & Allen 619* (FH, MO); Colón: *Crosby 4442* (F, MO, NY, PMA, US); Darién: *McPherson 12650E* (MO); Panamá: *Nee 10465* (DUKE, F, FH, MO, PMA, NY, US).

World range: Central America; Caribbean; Western and Northern South America.

Thamniopsis colombica differs from all other Central American species of *Thamniopsis* (except *T. guatemalensis* and *T. rivularis*) in its small, slender size: plants typically 1 cm long; leaves usually less than 1 mm; setae 4–10 mm long; capsules 0.5–1.0 mm long; and calyptrae 1 mm long. The species is placed in *Thamniopsis* on the basis of its stem hyalodermis, elimbate leaves, marginal teeth that can be somewhat swollen and bifid, enlarged, thin-walled basal cells, and massive annulus. Upper leaf cell areolation in *T. colombica* is one of its most distinctive features, but it varies considerably within single collections and at times on leaves from single plants. Typically, the dorsal and lateral leaves have isodiametric to hexagonal, thin-walled upper leaf cells, but these leaves can also have mostly long-rhomboidal upper cells. The ventral leaves are considerably different from the dorsal and lateral leaves in having lanceolate leaves, elongate upper leaf cells, and smooth costae that do not project at the tips.

Thamniopsis guatemalensis, *T. rivularis*, and *T. colombica* are similar in size, and in often having oval-hexagonal to rhomboidal-hexagonal upper leaf cells. The leaf cells of *T. guatemalensis* and *T. rivularis*, however, are narrower (5–10 µm vs. 10–20 µm) than those of *T. colombica*. *Thamniopsis guatemalensis* further differs from *T. colombica* in having leaves with somewhat bordered upper margins, an autoicous sexual condition, and smooth setae. *Thamniopsis rivularis* also differs from *T. colombica* in having leaves with single, unswollen marginal teeth and costae that do not project at the tips and are smooth at back.

Plants of *Cyclodictyon* are similar to in size to *Thamniopsis colombica*, and at times *T. colombica* has the pale green color commonly found in *Cyclodictyon*. In addition, both taxa have a stem hyalodermis and the same upper leaf cell areolation. All species of *Cyclodictyon* differ from *T. colombica* in having bordered leaves, smooth setae, and rudimentary annuli. *Thamniopsis colombica* is comparable in size to *Callicostella*, and it has been placed in that genus because it has elimbate leaves that are similar in shape. Furthermore, there are some *Callicostella* species with smooth cells; however, the large, hexagonal, thin-walled cells of *T. colombica* have no counterpart in that genus.

2. *Thamniopsis cruegeriana* (Müll. Hal.) W. R. Buck, Brittonia 39: 218. 1987. *Hookeria cruegeriana* Müll. Hal., Syn. Musc. Frond. 2: 208. 1851. *Hookeriopsis cruegeriana* (Müll. Hal.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 359. 1877. Protologue. Insula Trinidad Antillarum, monte Tamanaco, 1847. 10 Aug. *Crüger*.

Hookeriopsis killipii R. S. Williams, Bryologist 28: 62. 1925. *Thamniopsis killipii* (R. S. Williams) E. B. Bartram, Contr. U. S. Natl. Herb. 26(3): 103. 1928. Protologue. Colombia. Cordoba, Department of El Valle, Colombia. *E. P. Killip, 5246*, May 6–8, 1922. Types. Exploration in Colombia. Department of El Valle, Cordoba, Dagua Valley, Alt. 80–100 m, *Ellsworth P. Killip 5246* (FH, US, isotypes).

Hookeriopsis maguirei E. B. Bartram *in* Maguire *et al.*, Mem. New York Bot. Gard. 10(2): 9. 1960. Protologue. Venezuela: Amazonas: Cerro de la Neblina, locally frequent on logs and tree trunks in talus forest between Camps 3 and 4, alt. 700–1100 m, December 28, 1957, *Maguire, Wurdack & Maguire 42543a*. Type. N. Y. Bot. Garden Venezuelan Exped. 1957–58. Cerro de la Neblina, Rio Yatua, Territorio de Amazonas. Locally frequent on logs and tree trunks in talus forest between Camps 3 and 4. elev. 700–1100 m, *Basset Maguire, John J. Wurdack & Celia K. Maguire 42543a*. Dec. 28, 1957 (FH, holotype).

Hookeriopsis venezuelensis E. B. Bartram, Bol. Soc. Venez. Ci. Nat. 25: 40. 1963. Protologue. [Venezuela] Sierra Ichún: cercanías del Salto María Espuma (Salto Ichún) del río Ichún, base de la sierra de Ichún, tributario del río Paragua, Lat. 4° 46′: Long 68° 18′, on wet rocks along south side of river, 500 m, *Julián A. Steyermark 90369*. Type. Sierra Ichún: cercanías del Salto María Espuma (Salto Ichún) del río Ichún, base de la sierra de Ichún, tributario del río Paragua, Lat. 4° 46′; Long 68° 18′, altura 500 metros, on wet rocks along south side of river, *Julian A. Steyermark 90369* (FH, holotype), *syn. nov.*

Plants medium-sized to robust, 4–10 cm long, greenish, yellowish green, to golden, in dense mats. Stems prostrate, irregularly subpinnately branched, hyaline to yellowish when young, becoming reddish with age; stems in cross section with hyalodermis, subepidermis of 2–3 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia small, foliose; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions at base of costae and around branch primordia, smooth, reddish brown, not or sparsely and irregularly branched. Leaves extremely dimorphic, at times curved-imbricate or erect-spreading, smooth, ovate to oblong-ovate, 1.2–1.7 mm long, symmetric, rounded to obtuse, often bluntly mucronate, plane to concave; margins entire, plane or erect, marginal cells not forming a border; costae double, ending 2/3–3/4 the leaf length, diverging throughout or converging above, smooth or serrate-toothed at back, not projecting or weakly to strongly projecting at the tips, sometimes by multicellular spines; cells smooth, often porose, firm- to thick-walled, apical cells short-oblong, 6–14 µm long, median cells 26–70 µm long; basal cells enlarged, more or less bulging, thin-walled, oblong-rectangular; alar cells not differentiated; at other times erect to erect-spreading, smooth or undulate, ovate- to oblong-lanceolate, 1.5–2.0 mm long, symmetric, gradually to abruptly acuminate, occasionally blunt at the apex, plane to concave; margins sharply serrate in upper 2/3 by long or short, swollen, bifid cells, entire or subentire at base, plane or erect, marginal cells sometimes forming a weak, intramarginal border of narrow, elongate cells; costae double, ending 2/3–3/4 the leaf length, diverging throughout,

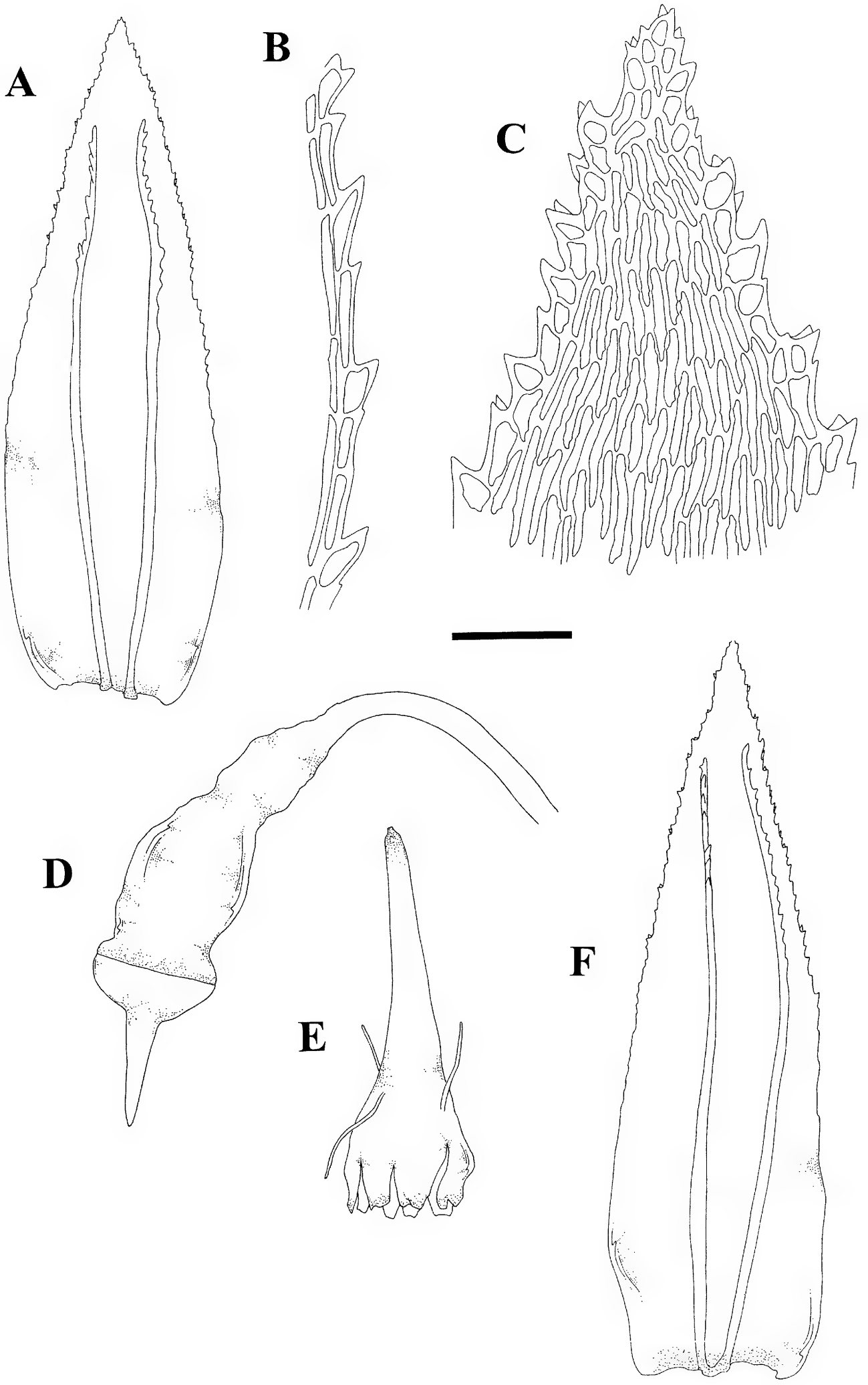


Figure 214. *Thamniopsis cruegeriana*. A & F. Leaves. B. Costal crest. C. Leaf apex. D. Seta, capsule, and operculum. E. Calyptra. Scale in mm: bar = 0.06 (B, C); bar = 0.36 (A, F); bar = 0.7 (D, E). D from *Allen 5592*; E from *McPherson 7251C*; all other figure parts from *Allen 5493*.

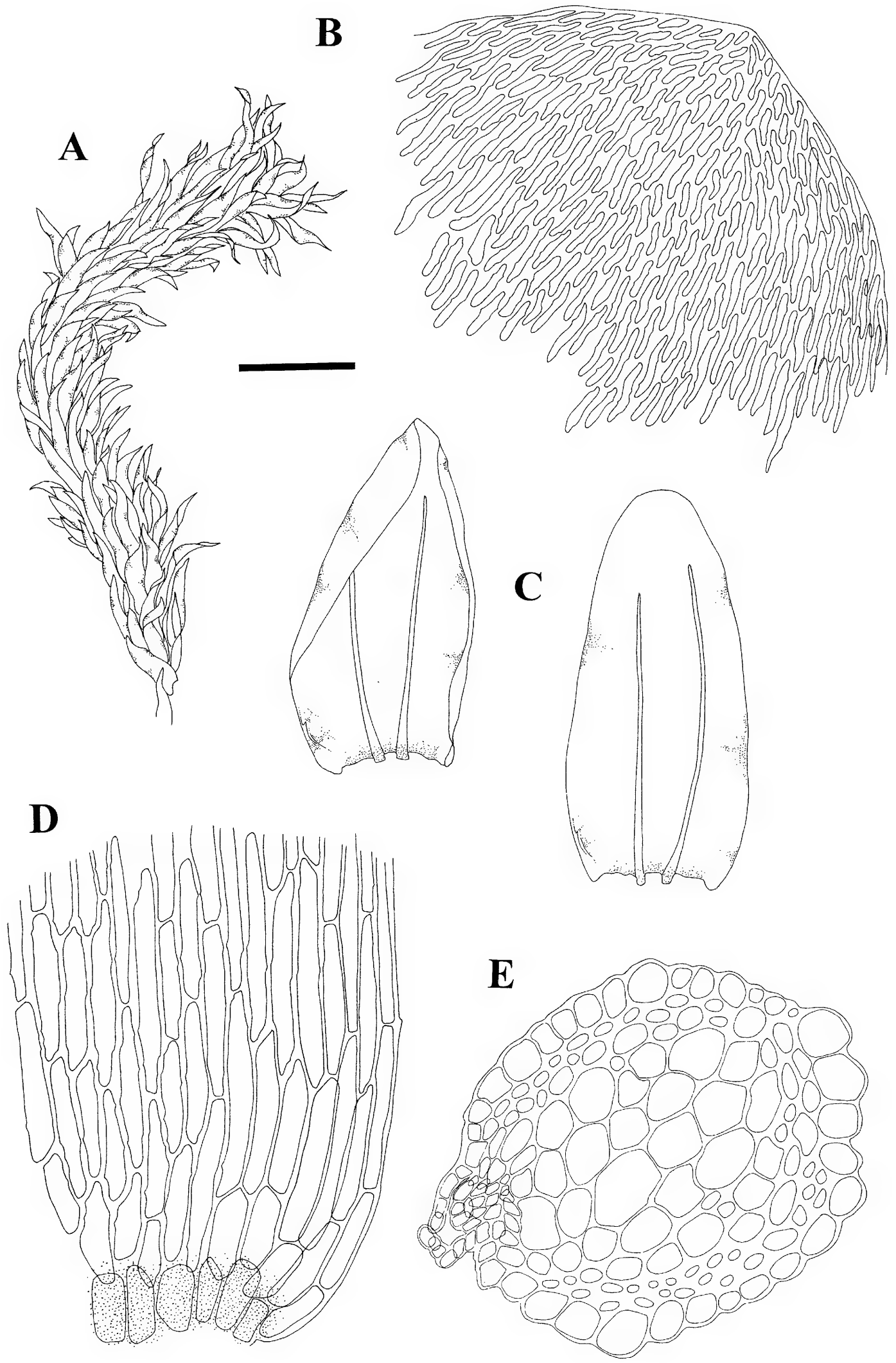
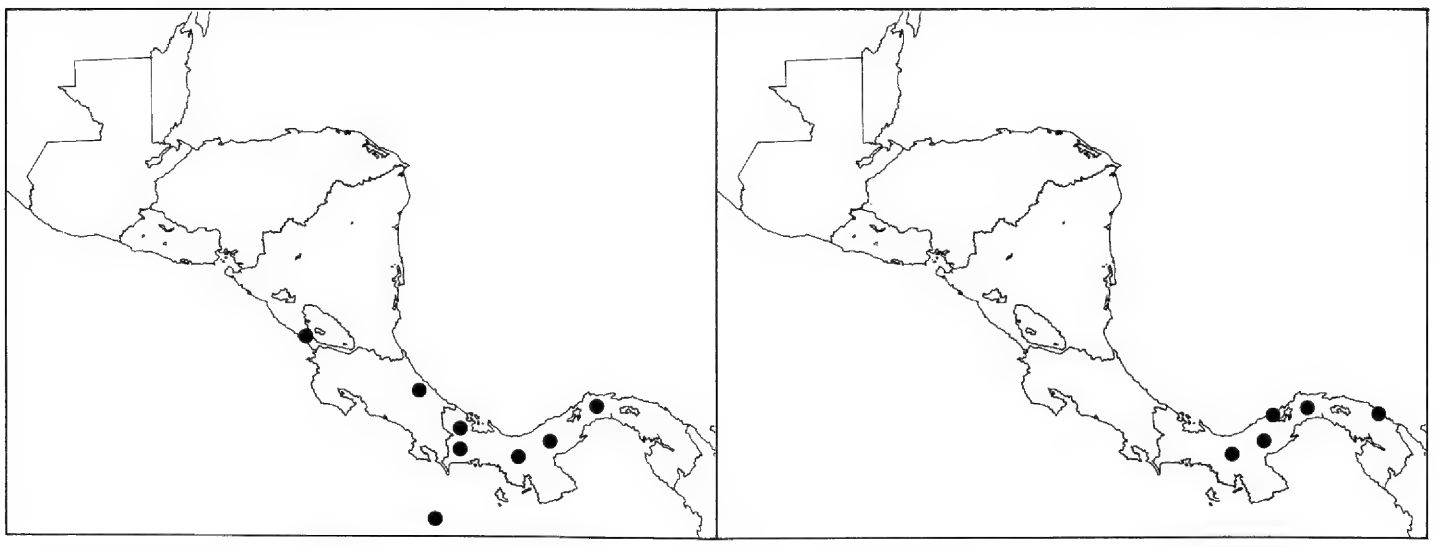


Figure 215. *Thamniopsis cruegeriana*. A. Habit. B. Leaf apex. C. Leaves. D. Basal and alar cells. E. Stem in cross section with pseudoparaphyllia. Scale in mm: bar = 0.06 (B, D); bar = 0.08 (E); bar = 0.36 (C); bar = 1.56 (A). All figure parts from *Allen 5493*.



Thamniopsis cruegeriana *Thamniopsis diffusa*

toothed at back, strongly projecting at the tips; cells smooth, often porose, firm- to thick-walled, extreme apical cells short-oblong, 10–16 µm long, median cells 32–60 µm long; basal cells enlarged, more or less bulging, thin-walled, oblong-rectangular; alar cells not differentiated. Dioicous. Setae elongate, 30–35 mm long, red, smooth throughout, or at times roughened on neck and below the capsules. Capsules horizontal to pendent, oblong-cylindric, 2.0–2.5 mm long, neck well developed; exothecial cells quadrate in 2–4 rows at mouth, those below oblong to rectangular, lateral walls evenly thickened, horizontal walls collenchymatous; stomata rudimentary, 3–4-celled, on neck; opercula long conic-rostrate, 1.0–1.5 mm long; annuli of 7–9 rows of thin-walled, quadrate to short-rectangular cells, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome narrowly triangular with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface dark red, densely and closely cross-striate below, coarsely papillose above, primary walls yellow, smooth, ventral (inner) surface hyaline to yellowish, deposition thin, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not or faintly perforate, cilia absent. Spores rounded, 10–14 µm, smooth to faintly papillose. Calyptrae mitrate, 2–3 mm long, yellowish white, irregularly lobed at base, sparsely hairy or smooth.

Illustrations. Bartram (1949, Fig. 136 A–C); Welch (1966, Figs. 139–143); Florschütz-de Waard (1986, Fig. 120, as *Thamniopsis killipii*); Sharp *et al.* (1994, Fig. 596); Churchill and Linares (1995, Fig. 45 a–d, as *Thamniopsis killipii*); Buck (1998, Pl. 8 1–13). Figures 214 & 215.

Habitat. On soil and humus, tree trunks, roots, and rotting logs or trunks; 400–1220 m.

Distribution in Central America. NICARAGUA. Rivas: *Moreno 19781* (HNMN, MO, NY, US). COSTA RICA. Limón: *Steere CR-99* (NY); Puntarenas: Cocos Island, *Dauphin 997* [Bryophyta Neotropica Exsiccata 372, as *Pilotrichum corrugatum*] (MO), *Svenson 347A* (FH). PANAMA. Bocas del Toro: *Allen 5632* (MO, PMA); Chiriquí: *Allen 5493* (MO); Coclé: *Sytsma 3975* (MO, NY, PMA, US); Panamá: *Crosby 10409* (MO, PMA); Veraguas: *Crosby 10191* (MO).

World range: Mexico; Central America; Caribbean; Western and Northern South America.

Thamniopsis cruegeriana is a medium-sized to robust species that exhibits an enormous, almost unbelievable, degree of leaf polymorphism. The leaves are sometimes smooth, ovate to oblong-ovate, with rounded to obtuse apices, entire margins, and weak costae that are usually smooth at back and do not project at the tips. At other times the leaves are undulate, ovate- to oblong-lanceolate with gradually to abruptly acuminate apices, sharply serrate margins (the teeth swollen and bifid), and strong costae that are spinose-toothed at back and strongly projecting at the tips. The distribution of these different leaf types on the plants is widely variable. In some collections the stem leaves are of the rounded-apex form while the branch leaves have the acuminate-apex form; in other collections the stem leaves again have the rounded-apex form but the branches can have both forms of leaves. In still other collections the stem leaves are of the acuminate-apex form and branch leaves can be of ei-

ther form. Furthermore, the change from one leaf form to another on a single stem or branch is remarkably abrupt, usually marked by just a few leaves that are transitional in form. Finally, the relative preponderance of a particular leaf type varies considerably from collection to collection. Collections that consist mostly of the acuminate-apex form and have the rounded-apex form restricted to the stems are typified by *Thamniopsis cruegeriana*. Collections that consist mostly of the rounded-apex leaf form and have the acuminate-apex leaf form restricted to a few branches represent what has been called *Thamniopsis killipii*. There are collections that exhibit nearly every variation between the two extremes. Robinson (1967) was the first to synonymize *T. killipii* and *T. maguirei* with *T. cruegeriana*.

In Central America *Thamniopsis cruegeriana* can be very difficult to distinguish from *T. pendula*, *T. oedodontia*, and *T. diffusa*. *Thamniopsis pendula* differs from *T. cruegeriana* in having only leaves that are ovate to oblong-ovate, with rounded to obtuse apices and entire margins. The leaves of *T. pendula* are identical in form to most of the rounded-apex leaves of *T. cruegeriana*. However, the rounded-apex leaves of *T. cruegeriana*, especially as they begin to transition to the acuminate leaf form, often have costae that converge above, are somewhat toothed at back, and have strongly projecting tips. In addition the two species have somewhat different perichaetial leaves: *T. pendula* nearly entire to slightly serrate; *T. cruegeriana* sharply serrate, the teeth short, swollen, often bifid. *Thamniopsis oedodontia* differs from *T. cruegeriana* in having only leaves with acuminate apices and massive, swollen, bifid marginal teeth. Although the acuminate leaves of *T. cruegeriana* can also have swollen, bifid marginal teeth, they are never as large and swollen as those of *T. oedodontia*. Furthermore, the leaves of *T. oedodontia* often have very weak costae that are very different from the strongly costate leaves of *T. cruegeriana*, and very long, linear-flexuose leaf cells. *Thamniopsis diffusa* is similar to *T. cruegeriana* in having strongly dimorphic leaves, and its leaves more or less parallel the variation seen in *T. cruegeriana*. It differs from *T. cruegeriana* in having some leaves with rounded apices that are bordered by quadrate to short-rectangular cells; well-developed intramarginal borders of narrow, elongate cells; and multicellular marginal teeth.

3. *Thamniopsis diffusa* (Wilson) W. R. Buck, Brittonia 39: 218. 1987. *Hookeria diffusa* Wilson *in* Seemann, Bot. Voy. Herald 245. 1854. Protologue. Panama. [*Berthold Seemann*] *1179*. Type. Panama, Pacific, *Seeman* [sic], 1847 (FH, isotype).

Plants medium-sized to robust, 4–10 cm long, greenish, yellowish green, to golden, in dense mats. Stems prostrate, irregularly subpinnately branched, hyaline to yellowish when young, becoming reddish with age; stems in cross section with hyalodermis, subepidermis of 2–3 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia small, foliose; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions at base of costae and around branch primordia, smooth, reddish brown, not or sparsely and irregularly branched. Dorsal and lateral leaves extremely polymorphic; at times leaves curved-imbricate or erect-spreading, smooth, ovate to oblong-ovate, 1.0–1.4 mm long, symmetric, rounded to obtuse, plane to concave; margins entire, plane or erect, marginal cells not forming a border; costae double, ending 2/3–3/4 the leaf length, diverging throughout or converging above, smooth or serrate-toothed at back, not projecting or weakly to strongly projecting at the tips, sometimes by multicellular spines; cells smooth, firm- to thick-walled, apical cells short-oblong, 12–20 µm long, median cells 18–30 µm long, cells along the costa enlarged and elongate, 60–100 µm long; basal cells enlarged, more or less bulging, thin-walled, oblong-rectangular; alar cells not differentiated; at other times erect to erect-spreading, smooth or undulate, ovate- to oblong-lanceolate, 1.4–1.8 mm long, symmetric, gradually to abruptly acuminate, acute, or truncate at the apex, plane to concave; margins serrate to dentate in upper 2/3, teeth sharp and often multicellular, entire or subentire at base, plane or erect, marginal cells forming a border of quadrate to short-rectangular cells, strong intramarginal border of narrow, elongate cells usually present; costae double, ending 2/3–3/4 the leaf length, diverging throughout, smooth or toothed at back, strongly projecting at the tips; cells smooth, often porose, firm- to thick-walled, extreme apical cells short-oblong in 2–5 rows, 14–18 µm long, median cells 14–40 µm long, cells along the costa enlarged and elongate, 60–100 µm long; basal cells enlarged, more or less bulging, thin-walled, oblong-rectangular; alar cells not differentiated. Ventral leaves ovate-lanceolate, gradually acuminate; mar-

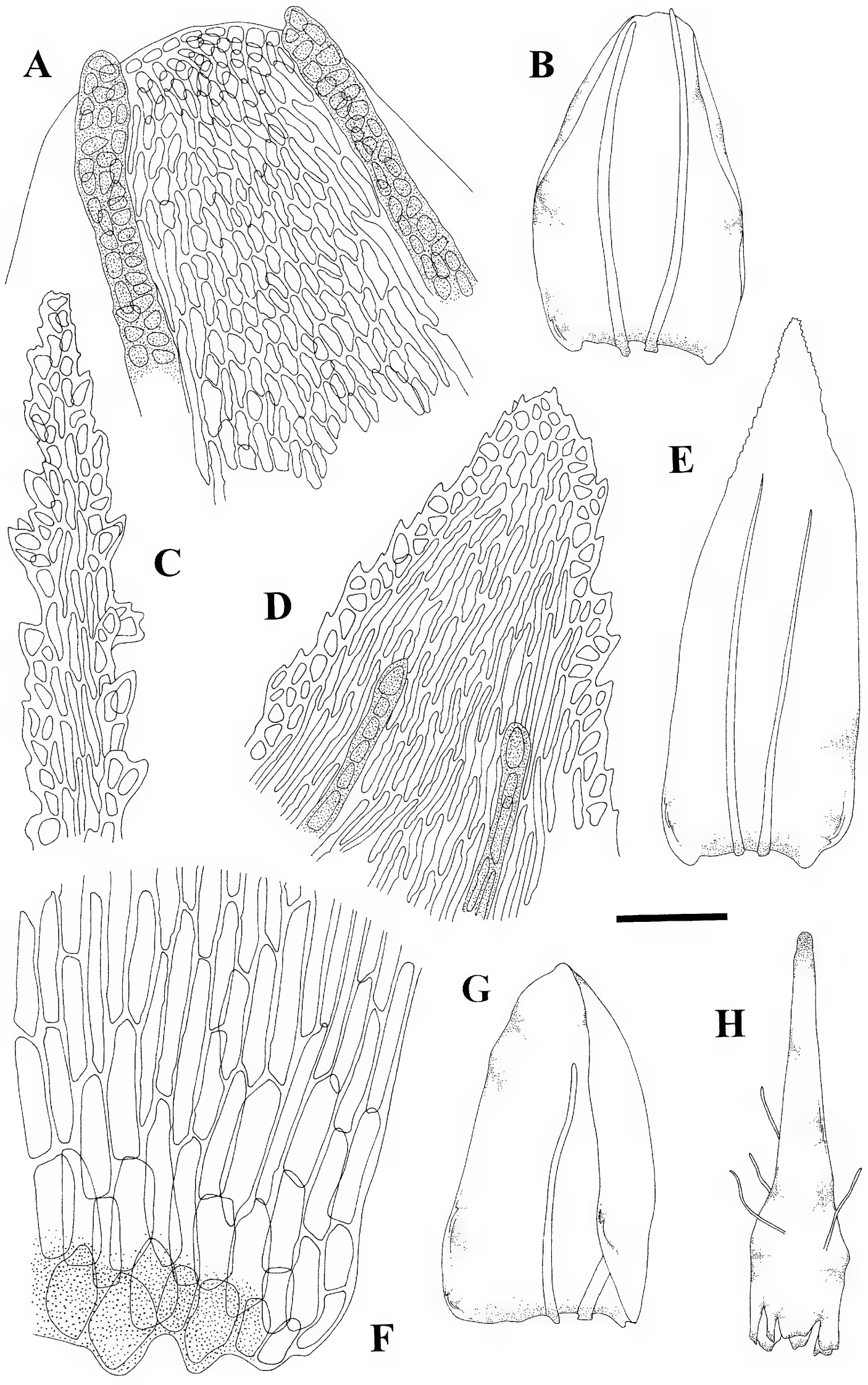


Figure 216. *Thamniopsis diffusa*. A. Leaf apex. B & G. Leaves. C. Perichaetial leaf apex. D. Leaf apex. E. Ventral leaf. F. Basal and alar cells. H. Calyptra. Scale in mm: bar = 0.06 (A, C, D, F); bar = 0.36 (B, E, G); bar = 0.6 (H). All figure parts from *Crosby 10894*.

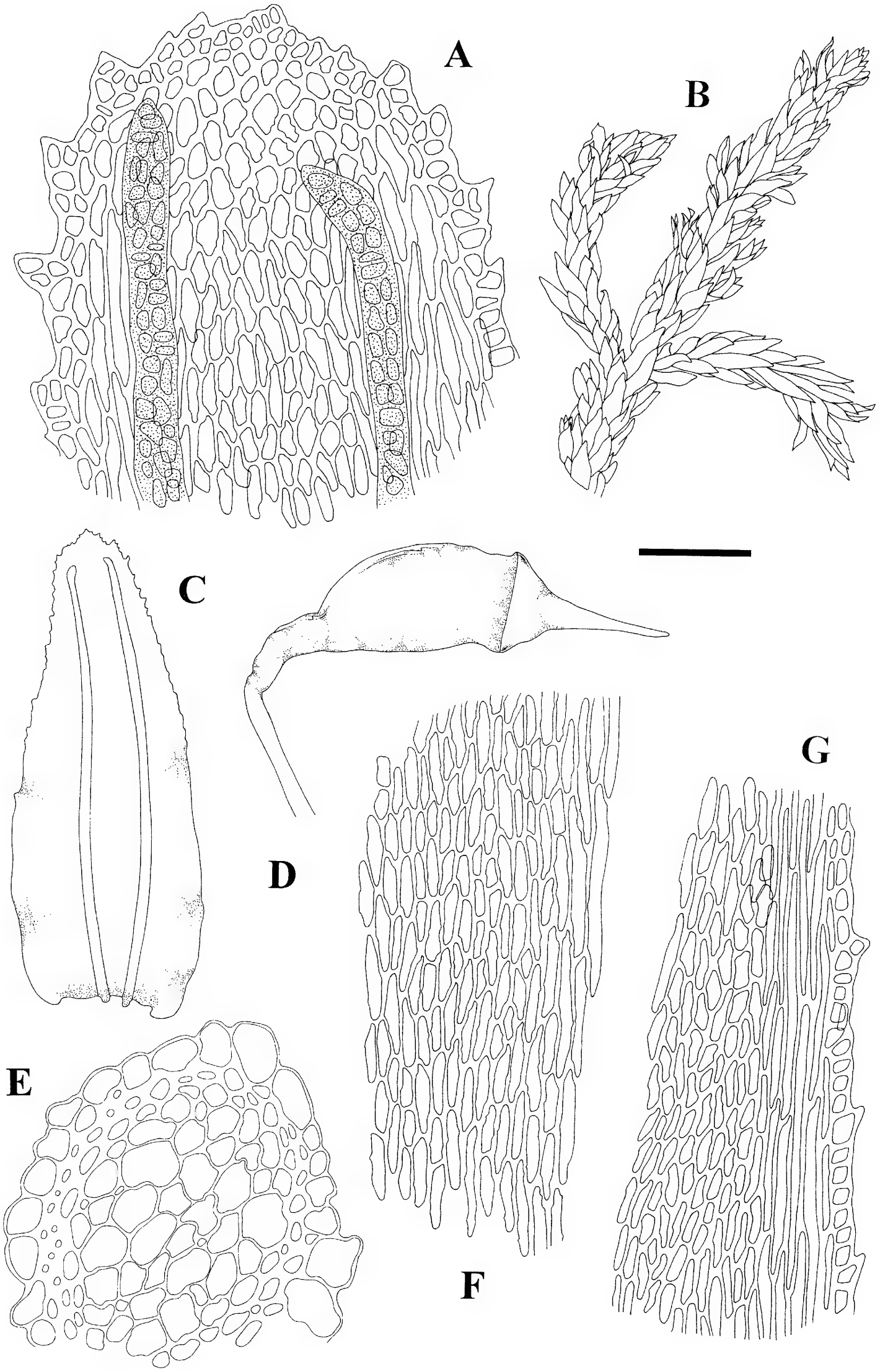


Figure 217. *Thamniopsis diffusa*. A. Leaf apex. B. Habit. C. Lateral leaf. D. Seta, capsule, and operculum. E. Stem in cross section. F. Median leaf cells near costa. G. Upper leaf cells and margin. Scale in mm: bar = 0.06 (A, F, G); bar = 0.08 (E); bar = 0.36 (C); bar = 0.9 (D); bar = 1.96 (B). All figure parts from *Crosby 10894*.

gins serrate by unicellular teeth; costae weak; all cells elongate, lax, thin-walled. Dioicous. Perichaetial leaves ovate below, long, narrowly acuminate above; margins sharply serrate to dentate, the teeth often bifid. Setae elongate, 25–30 mm long, red, smooth throughout, at times roughened on neck and below the capsules. Capsules horizontal to pendent, oblong-cylindric, 1.5–2.0 mm long, neck well developed; exothecial cells quadrate in 2–4 rows at mouth, those below oblong to rectangular, lateral walls evenly thickened, horizontal walls collenchymatous; stomata rudimentary, 3–4-celled, on neck; opercula long conic-rostrate, 1.0–1.5 mm long; annuli of 7–9 rows of thin-walled, quadrate to short-rectangular cells, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome narrowly triangular with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface dark red, densely and closely cross-striate below, coarsely papillose above, primary walls yellow, smooth, ventral (inner) surface hyaline to yellowish, deposition thin, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not or faintly perforate, cilia absent. Spores rounded, 10–14 µm, smooth to faintly papillose. Calyptrae mitrate, 2–3 mm long, yellowish white, irregularly lobed at base, sparsely hairy or smooth.

Illustrations. Welch (1974, Figs. 184–192); Churchill and Linares (1995, Fig. 44 g–k). Figures 216 & 217.

Habitat. On rotting logs, soil, or mud in seasonally submerged areas and along streams, rarely on rocks; 350–1000 m.

Distribution in Central America. PANAMA. Coclé: *Crosby 4391* (MO); Colón: *Crosby 10894* (BM, F, FH, MO, NY, PMA, US); Panamá: *Folsom et al. 6188* (MO, NY, PMA); San Blas: *Almeda et al 6508* (MO); Veraguas: *McPherson 7153A* (MO).

World range: Central America; Western South America.

Thamniopsis diffusa is a medium-sized to robust species with an aspect very similar to *T. cruegeriana*. Both species exhibit an astonishing degree of leaf polymorphism, and, although not seeming to be possible, the leaf dimorphism of *T. diffusa* is even greater than that of *T. cruegeriana*. As in some leaves of *T. cruegeriana* and all leaves in *T. pendula*, the leaves can be smooth, ovate to oblong-ovate, with rounded to obtuse apices, entire margins, and have weak or strong costae that are smooth or serrate at back and variously projecting at the tips. This leaf type in *T. diffusa* has a parallel form in *T. cruegeriana*, in which the costae are very strong, converge above, and strongly project as multicellular spines. At other times the leaves are crispate to undulate, ovate- to oblong-lanceolate, with gradually acuminate, acute, or broadly truncate apices. The margins in these leaves are sharply serrate with often multicellular teeth, and the strong costae are spinose-toothed at back and strongly project at the tips. These leaves are bordered by quadrate to short-rectangular cells, with well-developed intramarginal borders of the enlarged, elongate, thin-walled cells, and cells along the costae that are also distinctly enlarged and elongate. In addition, the cells at the tips of the leaves are rounded to shortly oblong. This last feature is especially pronounced in leaves that have broadly truncate apices. The branches and stems of *T. diffusa* with serrate leaves also have ovate-lanceolate ventral leaves that are gradually acuminate, with elongate, lax, thin-walled cells, margins serrate by unicellular teeth, and weak costae.

The distribution of the first two leaf types is variable. Parts of some collections have stem and branch leaves of one form, while other parts have stem and branch leaves of the other form. At times stem leaves have the rounded-apex form and the branches have the acuminate to truncate-apex form. Furthermore, the change from one leaf form to another on a single stem or branch is abrupt, usually marked by just a few leaves that are transitional in form. Finally, although the relative preponderance of a particular leaf type is also exceedingly variable from collection to collection, the acuminate to truncate-apex form is always the dominant form.

In Central America *Thamniopsis diffusa* can be confused with *T. cruegeriana*, *T. oedodontia*, or *T. pendula. Thamniopsis pendula* differs from *T. diffusa* in having only ovate to oblong-ovate leaves, with rounded to obtuse apices and entire margins. The leaves of *T. pendula* are identical in form to most of the rounded-apex leaves of *T. diffusa.* However, the rounded-apex leaves of *T. diffusa*, especially as they begin to transition to the acuminate leaf form, often have costae that converge above, are somewhat toothed at back, and have strongly projecting tips. In addition the two species have

different perichaetial leaves: *T. pendula* nearly entire to slightly serrate; *T. diffusa* sharply serrate, the teeth often bifid. *Thamniopsis oedodontia* differs from *T. diffusa* in having only leaves with acuminate apices and massive, swollen, bifid marginal teeth. *Thamniopsis diffusa* never has swollen, bifid marginal teeth. Furthermore, the leaves of *T. oedodontia* often have very weak costae. *Thamniopsis cruegeriana* and *T. diffusa* are similar in having strongly dimorphic leaves that are often more or less parallel in form. In *T. cruegeriana*, however, the leaves are never broadly truncate, are not bordered by quadrate to short-rectangular cells, do not have an intramarginal border of enlarged, elongate, thin-walled cells, have unicellular marginal teeth, and the cells along the costae are not much different from the median leaf cells.

4. *Thamniopsis glandulifera* (Hampe) B. H. Allen, *comb. nov.* Basionym: *Hookeria glandulifera* Hampe, Linnaea 32: 156. 1863. *Trachyxiphium glanduliferum* (Hampe) Churchill & Linares, Bibliot. José Jerónimo Triana 12: 261. 1995. Protologue. [Colombia] Hab. Bogota, Boqueron, 2800 m, in ramis arborum pendula, parce junio leg. *A. Lindig*.

Hookeria vaga Mitt., J. Linn. Soc., Bot. 12: 360. 1869. *Trachyxiphium vagum* (Mitt.) W. R. Buck, Brittonia 39: 221. 1987. Protologue. [Ecuador] Andes Quitenses, *Jameson*.

Hookeriopsis cubensis Thér., Mem. Soc. Cub. Hist. Nat. "Felipe Poey" 14: 368. 1940. Protologue. [Cuba] Sierra Maestra, La Bayamesa, associé au *Hookeriopsis undata* (*Ekman 7187 p.p.*); Pico Turquino [sic] associé à une hépatique (*Ekman 5470*). Type (see Buck 1987). *Ekman 5470* (lectotype).

Plants slender, 1–4 cm long. Leaves pale green to yellowish green, in thin mats. Stems prostrate, irregularly to subpinnately branched, hyaline to yellowish when young, becoming red with age, evenly foliate; stems in cross section with hyalodermis, subepidermal layer of 1–2 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia small, foliose; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect to erect-patent, flexuose-contorted when dry, erect-spreading when wet, monomorphic, oblong-lanceolate to ovate-lanceolate, 1.0–1.5 mm long, symmetric, abruptly constricted at base of acumina, concave; margins serrate to serrulate in upper 2/3, subentire below, plane to erect, not bordered; costae double, thin, ending 2/3 the leaf length, diverging throughout, usually unequal, smooth at back, often projecting at the apex; upper and median cells spiculose-papillose, papillae to 10 µm high, upper cells flexuose-elongate, 30–40 × 3–4 µm, firm-walled, not porose, lower cells enlarged, oblong-rectangular to long-rectangular, thin-walled, bulging near insertions, cells across the insertions short-rectangular; alar cells not differentiated. Autoicous. Setae elongate, 20–25 mm long, red, flexuose, smooth below, papillose to scabrose below the capsules. Capsules inclined to pendent, short-cylindric, 1–2 mm long, neck well developed; exothecial cells quadrate to oblate in 2–3 rows at mouth, those below oblong to rectangular, collenchymatous; stomata rudimentary, 4–6-celled, on neck; opercula conic-rostrate, 1.0 mm long; annuli of 7–9 rows of quadrate cells, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome narrowly triangular with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface orange, densely and closely cross-striate below, coarsely papillose above, primary walls yellowish hyaline, smooth, ventral (inner) surface hyaline to yellowish, deposition thin, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not perforate, cilia absent. Spores rounded, 8–14 µm, smooth to faintly roughened. Calyptrae mitrate, 2.0 mm long, yellowish below, reddish above, irregularly lobed at base, naked.

Illustrations. Thériot (1940, Pl. 55 6, as *Hookeriopsis cubensis*); Churchill and Linares (1995, Fig. 47 a–f); Buck (1998, Pl. 27 1–8, as *Trachyxiphium vagum*). Figure 218.

Habitat. On logs, rotting tree bases, and fern leaves; 1640–2100 m.

Distribution in Central America. COSTA RICA. Cartago: *Crosby & Crosby 5910* (MO); Heredia: *Crosby & Crosby 6052* (MO). PANAMA. Chiriquí: *Hammel 7456* (MO).

World range: Central America; Caribbean; Western South America.

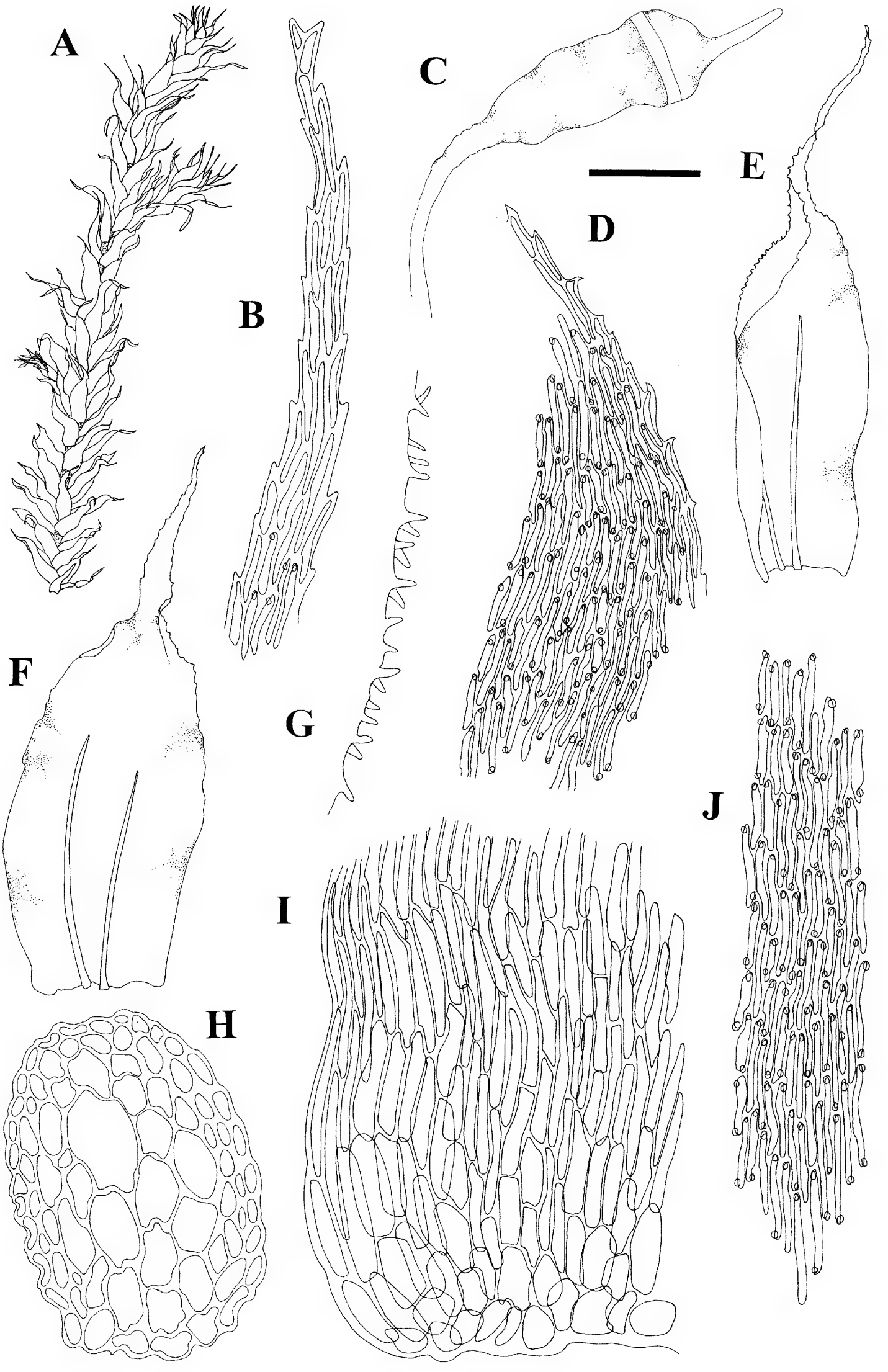
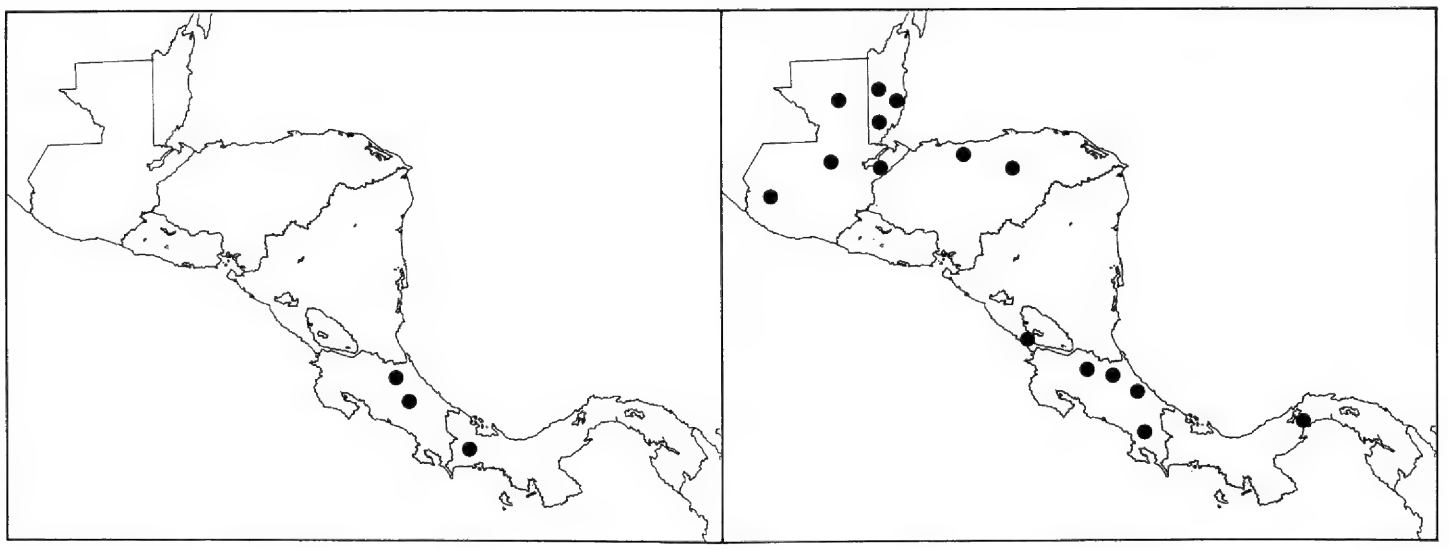


Figure 218. *Thamniopsis glandulifera*. A. Habit. B. Leaf apex. C. Seta, capsule, annulus, and operculum. D. Upper leaf cells and margin. E & F. Leaves. G. Leaf papillae in side view. H. Stem in cross section. I. Basal and alar cells. J. Median leaf cells. Scale in mm: bar = 0.05 (B, D, G, I, J); bar = 0.08 (H); bar = 0.6 (C); bar = 0.7 (E, F); bar = 1.56 (A). C from *Crosby 6052*; E, F from *Jameson 178* (type *Hookeria vaga*); all other figure parts from *Hammel 7456*.



Thamniopsis glandulifera *Thamniopsis guatemalensis*

Thamniopsis glandulifera is a slender species with evenly foliate, green to yellowish green leaves that are erect to erect-patent when dry. Its stems have a weakly developed hyalodermis and ovate-lanceolate to oblong-lanceolate leaves that are abruptly constricted at the base to long, slender acumina. The upper leaf margins in *T. glandulifera* are sharply serrate, and the flexuose-elongate cells have tall, spiculose papillae from both cell ends. The spiculose papillae can be 10 µm high. The basal leaf cells are enlarged, variously rectangular, and considerably differentiated from the upper leaf cells.

There are four *Thamniopsis* species in Central America with monomorphic leaves that are abruptly constricted at the base of the acumina: *T. glandulifera*, the *acicularis*-form of *T. undata*, *T. purpureophylla*, and *T. steyermarkii*. *Thamniopsis glandulifera* differs from the others in having high, spiculose-papillose leaf cells. The *acicularis*-form of *T. undata* furthers differs from *T. glandulifera* in having larger, undulate leaves (2.5–4.0 mm vs. 1.0–1.5 mm long), broader upper leaf cells (3–14 µm vs. 3–4 µm), and somewhat swollen marginal teeth. *Thamniopsis glandulifera*, *Thamniopsis steyermarkii*, and *T. purpureophylla* are nearly identical in size, leaf shape, and leaf cell form. *Thamniopsis steyermarkii* is also similar to *T. glandulifera* in having a green or yellowish color, but its leaf cells are consistently smooth. *Thamniopsis purpureophylla* has low, prorate leaf cells, and its plants are reddish purple in color. Plants of *T. glandulifera* are remarkably similar to *Hypnella pilifera* in color, leaf shape, and cell form. Furthermore, the leaf cells of *Hypnella pilifera* often have high, curved papillae comparable to those of *T. glandulifera*. The leaf cells in *H. pilifera*, however, are pluripapillose with 2–6 more or less seriately arranged papillae.

5. *Thamniopsis guatemalensis* (E. B. Bartram) B. H. Allen, *comb. nov*. Basionym: *Hookeriopsis guatemalensis* E. B. Bartram, Bryologist 49: 120. 1946. *Schizomitrium guatemalensis* [*e*] (E. B. Bartram) J. Florsch., Fl. Suriname 6(1, II): 326. 1986. Protologue. [Guatemala] Dept. Izabal: between Bananera and "La Prensa" in Montaña del Mico, alt. 40–300 m, *Steyermark 38243*. Types. Guatemala. Dept. Izabal: between Bananera and "La Prensa" in Montaña del Mico, alt. 40–300 m. March 28, 1940, *Julian A. Steyermark 38243* (FH, holotype; NY, isotype).

Plants small and slender, 1–4 cm long, pale greenish, green, or reddish, in dense or loose mats. Stems prostrate, irregularly branched, hyaline to yellowish when young, becoming reddish with age; stems in cross section with moderate-sized hyalodermis, subepidermis of 2–3 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent, but with foliose scaly leaves; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Lateral and dorsal leaves erect-flexuose to crispate when dry, erect-spreading when wet, oblong-ovate to oblong-lanceolate, 0.9–1.2 mm long, acute to short-acuminate; margins serrate to dentate in upper 2/3, teeth slightly swollen, often bifid, entire below, plane to erect; costae double, ending 2/3–3/4 the leaf length, diverging throughout, unequal, often serrate on back, projecting at the apex; cells smooth,

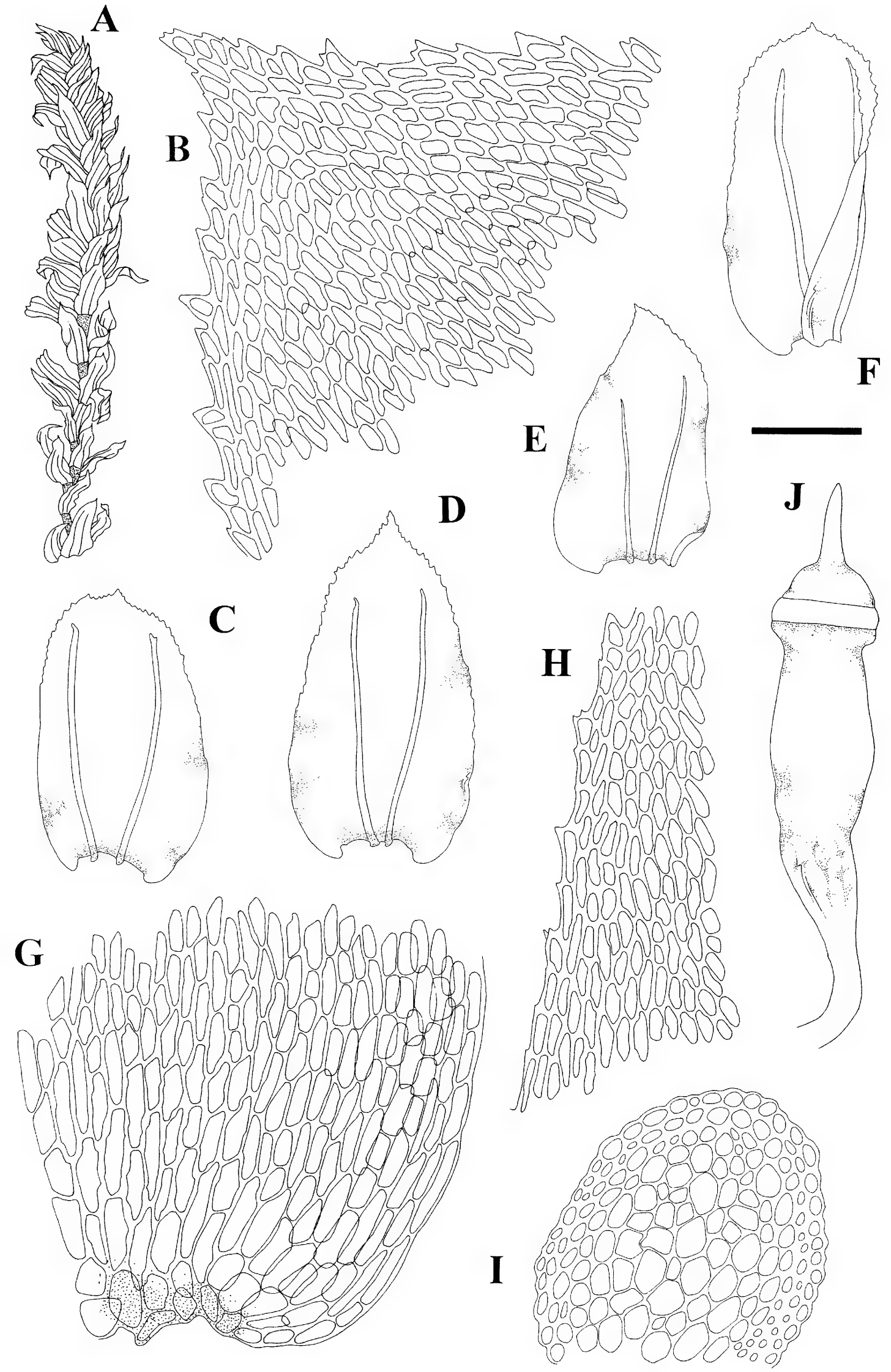


Figure 219. *Thamniopsis guatemalensis*. A. Habit. B. Leaf apex. C–F. Leaves. G. Basal and alar cells. H. Upper leaf cells and margin. I. Stem in cross section. J. Seta, capsule, annulus, and operculum. Scale in mm: bar = 0.06 (B, G, H); bar = 0.08 (I); bar = 0.36 (C–F); bar = 0.5 (J); bar = 1.56 (A). All figure parts from *Steyermark 38243* (type).

upper cells oval-hexagonal to long-rhomboidal, 14–32 × 5–10 µm, firm-walled, usually eporose but occasionally slightly porose, lower cells elongate-rhomboidal to long-rectangular; basal cells near the insertions enlarged, oblong-rectangular; alar cells not differentiated. Ventral leaves erect, ovate-lanceolate, 1.2 mm long, symmetric, short-acuminate; margins serrate in upper 2/3, teeth elongate, rarely bifid, entire below; costae double, slender, ending 2/3 the leaf length, diverging throughout, unequal, smooth on back, not projecting at the apex; upper cells elongate-flexuose. Autoicous. Setae elongate, 10–15 mm long, red, flexuose, smooth. Capsules horizontal, short-cylindric, 1.0–1.5 mm long, neck well developed; exothecial cells quadrate to oblate in 2–4 rows at mouth, those below oblong to rectangular, lateral walls evenly thickened, horizontal walls collenchymatous; stomata rudimentary, on neck; opercula conic-rostrate, 0.7 mm long; annuli of 7–9 rows of cells, lower cells transversely rectangular, upper cells quadrate, all cells thin-walled with irregular nodose thickenings, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome narrowly triangular with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface dark red, densely and closely cross-striate below, coarsely papillose above, primary walls yellow, smooth, ventral (inner) surface hyaline to yellowish, deposition thin, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not or faintly perforate, cilia absent. Spores rounded, 9–12 µm, smooth to faintly roughened. Calyptrae mitrate, 1.5 mm long, yellowish white, red above, irregularly lobed at base, smooth.

Illustrations. Bartram (1949, Fig. 136 G–I); Welch (1974, Figs. 193–202); Florschütz-de Waard (1986, Fig. 127). Figure 219.

Habitat. On logs, rotting wood, wet banks, and limestone tufa; 40–2250 m.

Distribution in Central America. BELIZE. Cayo: *Allen 15148* (MO); Stann Creek: *Gentle 2812C* (NY); Toledo: *Allen 18805* (MO). GUATEMALA. Alta Verapaz: *Steyermark 45209* (F, FH, MO, NY); Izabal: *Steyermark 38243* (FH); Petén: *Steyermark 45381* (F, FH, MO, NY, US); Quetzaltenango: *Spellman et al. B111b* (MO). HONDURAS. Atlántida: *Allen 17471* (MO); Olancho: *Allen 12540* (MO). NICARAGUA. Rivas: *Granzow de la Cerda GC-1668* (DUKE, MO). COSTA RICA. Alajuela: *Dauphin 2325* (MO); Heredia: *Hammel 7899* (MO); Limón: *Daly 123* (MO); Puntarenas: *Bowers 281d* (MO). PANAMA. Canal Area: *Nee & Smith 11368* (MO).

World range: Central America; Northern South America.

Thamniopsis guatemalensis is a small species with short, oblong-ovate to oblong-lanceolate dorsal and lateral leaves, somewhat bordered upper leaf margins with swollen, often bifid teeth, oval-hexagonal to rhomboidal-hexagonal upper leaf cells, and costae that project at the tips and are often serrate on back. It was originally compared to *T. diffusa* (both in *Hookeriopsis*), but the species is much more similar to *T. colombica*. *Thamniopsis colombica* and *T. guatemalensis* differ from all other Central American species of *Thamniopsis* in their small, slender size: plants mostly 1 cm long; leaves less than 1.2 mm long; setae 4–15 mm long; capsules 0.5–1.5 mm long; and calyptrae 1.0–1.5 mm long. In size and overall aspect *T. guatemalensis* is very similar to the smooth-celled species of *Callicostella*, and it is sometimes placed in that genus. The species is here placed in *Thamniopsis* on the basis of its stem hyalodermis, marginal teeth that are often somewhat swollen and bifid, enlarged, thin-walled basal cells, costae serrate at back, and massive, persistent annulus. The oval-hexagonal to rhomboidal-hexagonal upper leaf cells of *T. guatemalensis* separate it from all other Central American species of *Thamniopsis* except for *T. colombica*, but in that species the cells are much wider (10–20 µm vs. 5–10 µm). The leaves of *T. colombica* further differ from those of *T. guatemalensis* in lacking a leaf border. In addition, *T. colombica* is dioicous and has scabrous setae. The ventral leaves in *T. guatemalensis* are considerably different from the lateral and dorsal leaves in their lanceolate shape, more elongate upper leaf cells, and smooth costae that do not project at the tips. *Thamniopsis rivularis* is similar to *T. guatemalensis* in overall aspect, and both species grow on rocks in and along streams. *Thamniopsis rivularis* differs from *T. guatemalensis* in having non-swollen, single teeth on the upper leaf margins, a dioicous sexual condition, and setae that are scabrous throughout.

Among the smooth-celled species of *Callicostella*, *T. guatemalensis* is most similar to *C. merkelii* in size, leaf shape, and leaf cell form. This species differs from *T. guatemalensis* in having a stem

sclerodermis, distinctive, foliose pseudoparaphyllia, and leaves with single, unswollen serrulate marginal teeth as well as very strong costae that are typically convergent at the tips.

6. *Thamniopsis incurva* (Hornsch.) W. R. Buck, Brittonia 39: 218. 1987. *Chaetophora incurva* Hornsch. *in* Nees, Horae Phys. Berol. 65. 1820. *Hookeria incurva* (Hornsch.) Hook. & Grev., Edinburgh J. Sci. 2: 231. 1825. *Lepidopilum incurvum* (Hornsch.) Müll. Hal., Linnaea 21: 195. 1848. *Callicostella incurva* (Hornsch.) Broth., Nat. Pflanzenfam. I(3): 942. 1907. Protologue. [Chile] Habitat in regno Chilensi ad truncos arborum detecta ab *Adalberto a Chamisso*.

Plants medium-sized to large, 3–6 cm long, pale greenish, green, or yellowish red, in dense mats. Stems prostrate, irregularly branched, hyaline to yellowish when young, becoming reddish with age, complanate-foliate; stems in cross section with hyalodermis, subepidermis of 2–3 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia filamentous, with foliose scale leaves; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves flattened, erect to spreading, somewhat contorted when dry, dimorphic. Lateral leaves wide-spreading, oblong to oblong-ovate, 1.5–2.5 mm long, asymmetric, broadly obtuse, plane to weakly concave; margins serrate in upper 2/3, entire below, teeth swollen, cells rounded, mostly bifid, broadly incurved on one side at base, otherwise plane, lower marginal cells elongate-rectangular, forming an obscure border 1–2 cells wide; costae double, thin, ending 1/2–2/3 the leaf length, diverging throughout, unequal, smooth on back, often projecting at the apices by a single, swollen cell; cells smooth, upper cells hexagonal to rhomboidal, 50–90 × 20–26 µm, firm-walled, at times porose, lower cells elongate-rhomboidal; basal cells near the insertions oblong-rectangular to long-rectangular, often porose; alar cells not differentiated. Dorsal and ventral leaves erect, ovate to obovate, 1–2 mm long, symmetric, obtuse to rounded-acute. Autoicous. Setae elongate, 20–30 mm long, red, smooth below, papillose-roughened to tubular-roughened on neck and upper part of setae. Capsules horizontal, oblong-cylindric, 2–3 mm long, neck well developed; exothecial cells quadrate in 2–4 rows at mouth, those below oblong to rectangular, lateral walls evenly thickened, horizontal walls collenchymatous; stomata rudimentary, on neck; opercula conic-rostrate, 1 mm long; annuli of 10–20 rows of cells, lower cells transversely rectangular, upper cells quadrate, all cells thin-walled with irregular nodose thickenings, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome narrowly triangular with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface dark red, densely and closely cross-striate below, coarsely papillose above, primary walls yellow, smooth, ventral (inner) surface hyaline to yellowish, deposition thin, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not or faintly perforate, cilia absent. Spores rounded, 12–18 µm, faintly papillose. Calyptrae mitrate, 3.0–3.5 mm long, yellowish white, often streaked with red, irregularly lobed at base, sparsely hairy.

Illustrations. Hornschuch (1820, Pl. 13); Brotherus (1907a, Fig. 685 A–C); Brotherus (1925, Fig. 604 A–C); Bartram (1949, Fig. 137 A–C); Welch (1969, Figs. 112–119); Sharp *et al.* (1994, Fig. 594); Duarte Bello (1997, Pls. 246 & 247); Buck (1998, Pl. 7); Vaz and Costa (2006b, Figs. 99–107). Figure 220.

Habitat. On rotting logs, bare soil, and rocks in forests or along streams, occasionally at base of trees and shrubs; 80–1098 m.

Distribution in Central America. BELIZE. Cayo: *Allen 15143* (BRH, MO); Toledo: *Allen 18791* (BRH, MO). GUATEMALA. Alta Verapaz: *Steyermark 44790* (F, FH, NY). HONDURAS. Atlántida: *Liesner 26293* (MO, TEFH). COSTA RICA. Cartago: *Standley & Valerio 47147* (FH, NY, US); Limón: *Standley 37487* (FH, NY, US). PANAMA. Panamá: *Crosby 10072* (MO); Veraguas: *Crosby 10289* (MO, PMA).

World range: Mexico; Central America; Caribbean; Western, Northern, and Southern South America, Brazil.

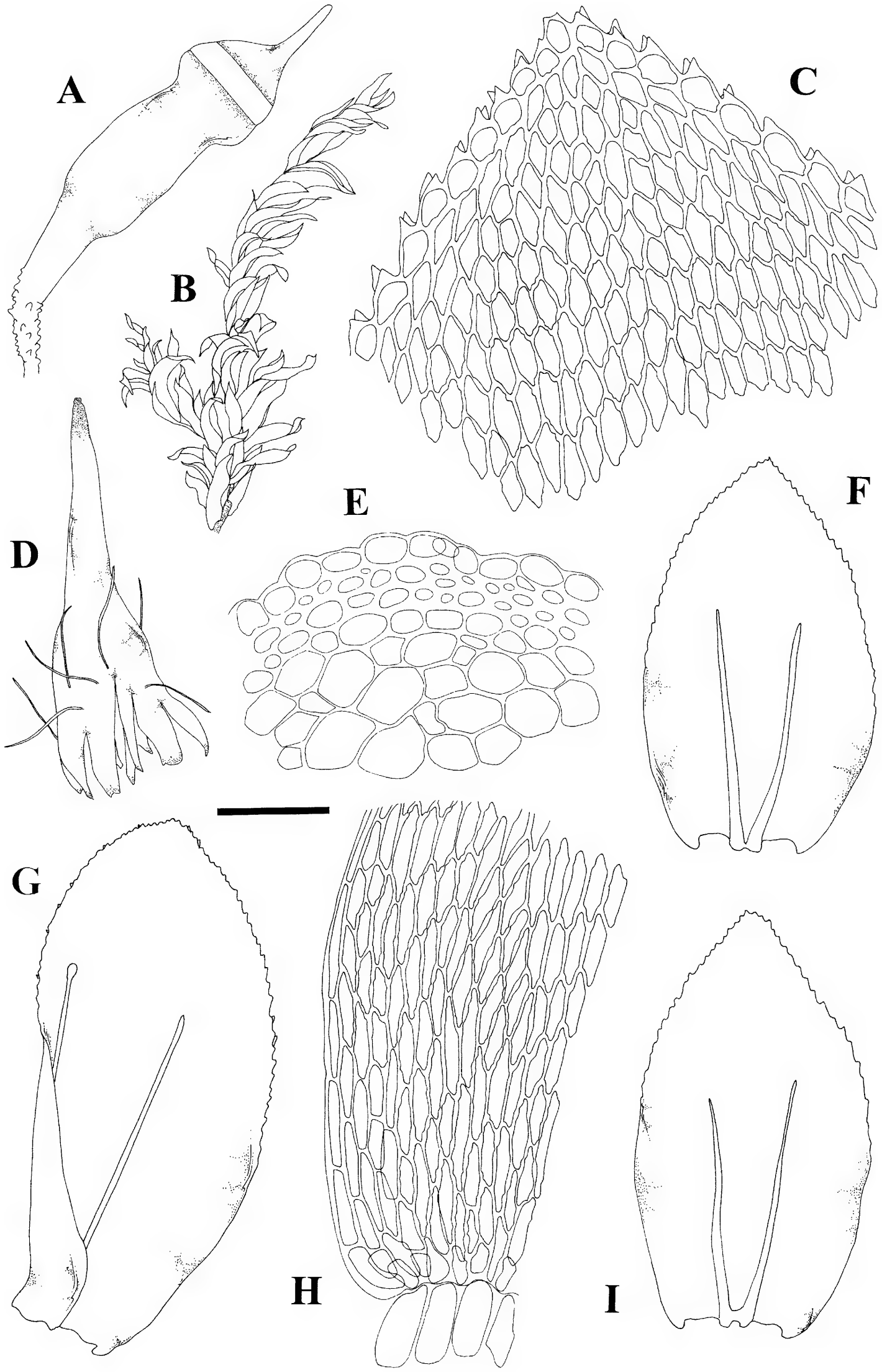
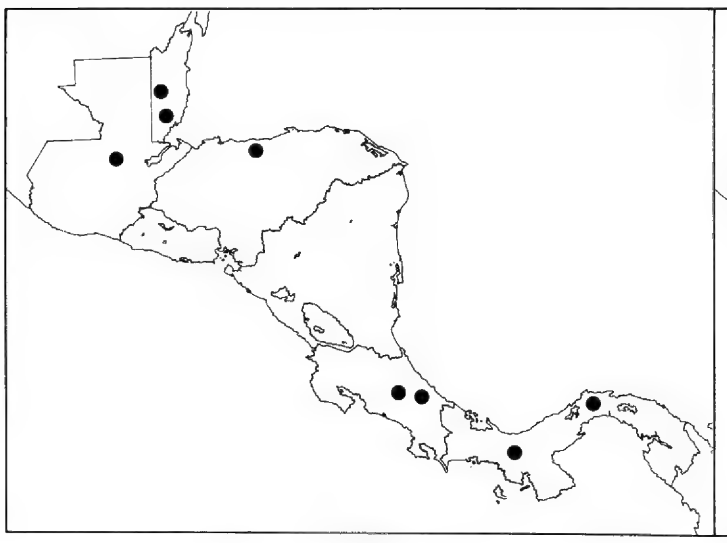
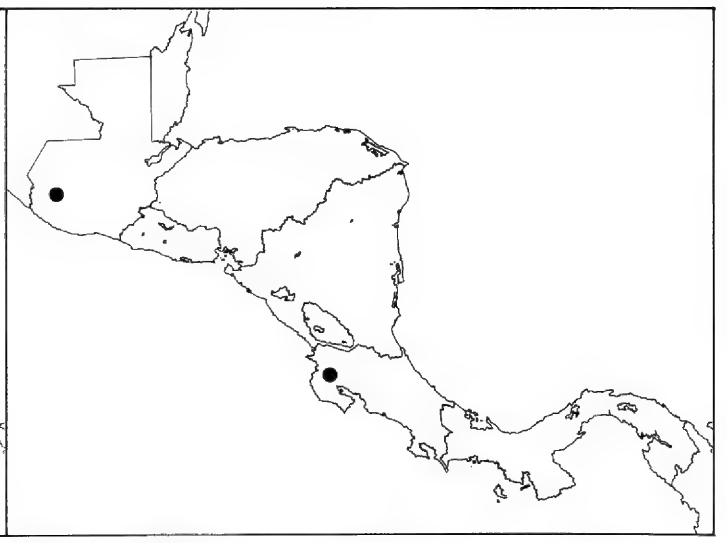


Figure 220. *Thamniopsis incurva*. A. Seta, capsule, annulus, and operculum. B. Habit. C. Leaf apex. D. Calyptra. E. Stem in cross section. F & I. Dorsal leaves. G. Lateral leaf. H. Basal and alar cells. Scale in mm: bar = 0.08 (E); bar = 0.13 (C, H); bar = 0.5 (F, G, I); bar = 0.9 (A, D); bar = 2.0 (B). A, D from *Allen 15143*; all other figure parts from *Allen 18791*.



Thamniopsis incurva



Thamniopsis oedodontia

Thamniopsis incurva is a fairly large species usually found in dense mats on rotting logs. It typically has greenish plants that are reddish tinged; at times they can be purplish red throughout. The stems of *T. incurva* are complanate-foliate with leaves that are variously contorted when dry, but when wet the asymmetric lateral leaves are wide-spreading, while the symmetric dorsal and ventral ones are erect. Distinctive gametophytic features of *T. incurva* include its thin-walled, filamentous pseudoparaphyllia; ovate, obovate, or oblong leaves that are obtuse to broadly rounded; weak, smooth costae that diverge throughout and usually end as a swollen, projecting cell; and broad, rhomboidal leaf cells. The leaves of *T. incurva* have biserrate margins with short, very swollen cells, and this is an especially diagnostic feature of the species.

The sporophytes of *T. incurva* have perfect hookeriaceous peristomes identical in form to those of *Cyclodictyon*. Its exothecial cells have evenly thickened lateral walls, and, while the horizontal walls are usually thin, they often have collenchymatous thickenings. The overall aspect of the exothecial cells, however, is one of sheets of cells with evenly thickened lateral walls rather than masses of collenchymatous cells. The annulus in *T. incurva* is massive and consists of 10–20 rows of large, yellowish cells. The layers near the capsule mouth are transversely rectangular, while those near the operculum are quadrate. All the cells are thin-walled with nodose thickenings here and there. Capsule dehiscence occurs at the base of the annulus along a line contiguous with the thick-walled cells of the capsule mouth. The annulus is persistent on the operculum, and both often fall with the calyptra. The calyptrae are large, mitrate, irregularly lobed at base, and sparsely hairy.

The presence on the upper leaf margins of *Thamniopsis incurva* of short, massive, greatly swollen, bifid teeth separates it from all other Central American species of *Thamniopsis* except *T. oedodontia*. Indeed, the bifid marginal teeth in both species are identical in form. *Thamniopsis oedodontia* differs from *T. incurva* in having symmetric, ovate-lanceolate lateral leaves with acuminate to narrowly acute apices. Furthermore, the costae of *T. oedodontia* are often spinose-toothed at back and its leaf cells are long and linear-flexuose.

7. *Thamniopsis oedodontia* B. H. Allen, *sp. nov*. Type. Costa Rica. Guanacaste: Parque Nacional Guanacaste Estación Cacao. Liberia. 10°55′45″N, 85°28′15″W, *Chávez 305* (MO, holotype; CR, FH, isotypes).

Species haec a *Thamniopse incurva* foliis symmetricis, ovatis-lanceolatis, acutis vel acuminatis cellulisque superis elongatis et ab aliis *Thamniopsibus* speciebus in Centralia America dentibus marginalibus in foliis multum tumidis differt.

Plants medium-sized to robust, 3–6 cm long, greenish, yellowish green, to golden, in dense mats. Stems prostrate, irregularly subpinnately branched, hyaline to yellowish when young, becoming reddish with age; stems in cross section with hyalodermis, subepidermis of 2–3 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudo-

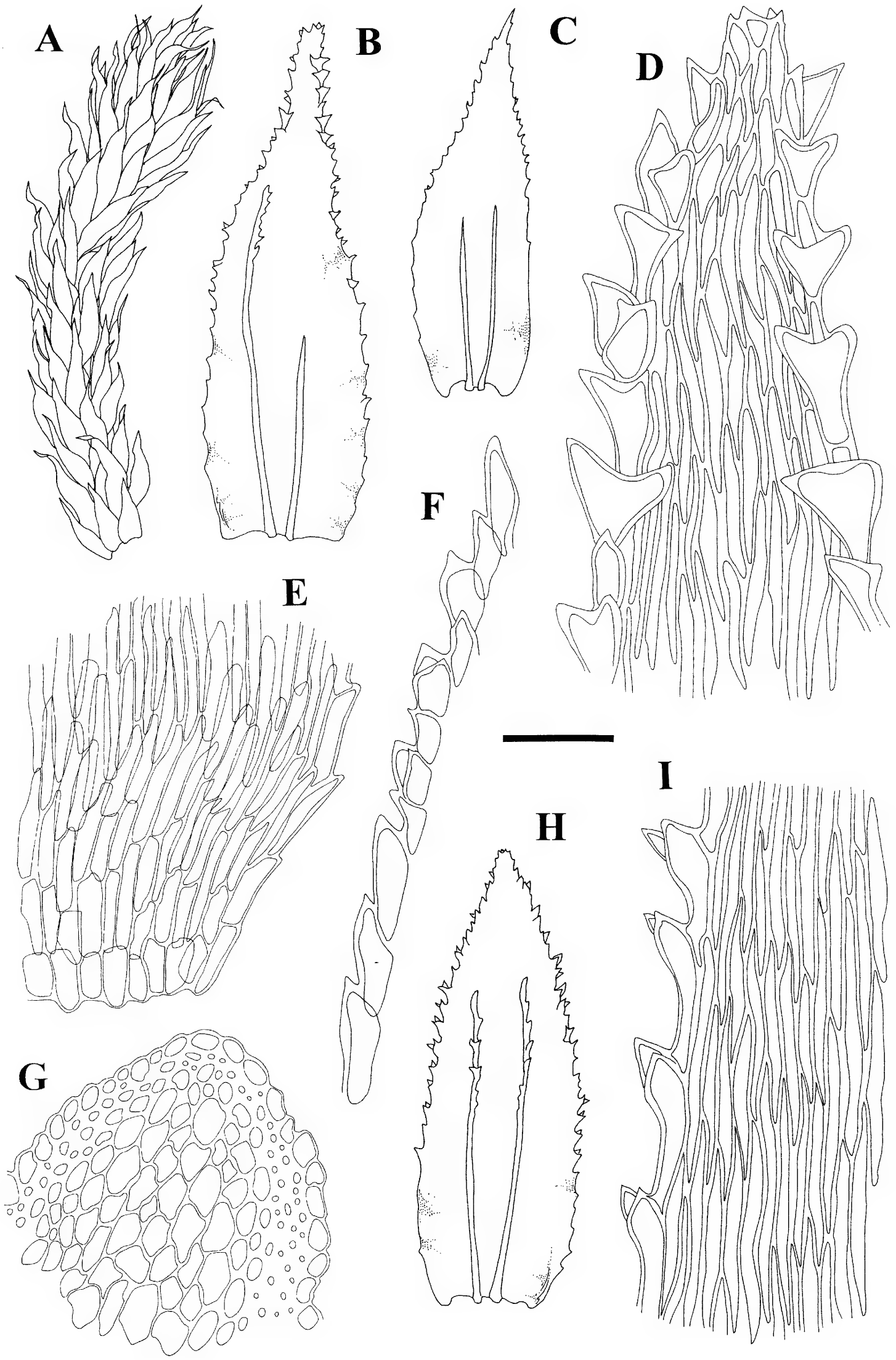


Figure 221. *Thamniopsis oedodontia*. A. Habit. B. Lateral leaf. C. Ventral leaf. D. Leaf apex. E. Basal and alar cells. F. Costal crest. G. Stem in cross section. H. Dorsal leaf. I. Upper leaf cells and margin. Scale in mm: bar = 0.06 (D, F, I); bar = 0.08 (E, G); bar = 0.4 (B, C, H); bar = 1.56 (A). All figure parts from *Chávez 305* (type).

paraphyllia small, foliose; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves monomorphic, erect-spreading, somewhat crispate to lightly undulate when dry, erect to erect-spreading when wet, ovate- to oblong-lanceolate, 1.4–1.8 mm long, symmetric, gradually to abruptly acuminate, occasionally blunt at the apex, flat to concave; margins sharply serrate in upper 2/3 by greatly enlarged, swollen, bifid teeth, serrulate at base, plane or erect, not bordered; costae double, diverging throughout, on lateral and dorsal leaves ending 1/2–2/3 the leaf length, variously spinose at back by swollen, bifid teeth, strongly projecting at tips, on ventral leaves ending 1/4 the leaf length, smooth at back, not projecting at the tips; cells smooth, thin-walled, not porose, linear-flexuose throughout, upper cells 90–100 × 6–10 µm, median and basal cells 100–180 × 6–10 µm, enlarged, more or less bulging, often porose, oblong-rectangular near the insertions; alar cells not differentiated. Dioicous. Setae elongate, 15–20 mm long, red, smooth throughout, or at times roughened on neck and below the capsules. Capsules horizontal to pendent, oblong-cylindric, 1.5–2.0 mm long, neck well developed; exothecial cells quadrate in 2–4 rows at mouth, those below oblong to rectangular, lateral walls evenly thickened, horizontal walls collenchymatous; stomata rudimentary, 3–4-celled, on neck; opercula long conic-rostrate, 0.75 mm long; annuli of 2–3 rows of thin-walled, quadrate to short-rectangular cells, separating from capsule along dehiscent zone at base, and persistent on the operculum; peristome diplolepideous, exostome narrowly triangular with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface dark red, densely and closely cross-striate below, coarsely papillose above, primary walls yellow, smooth, ventral (inner) surface hyaline to yellowish, deposition thin, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not or faintly perforate, cilia absent. Spores rounded, 10–12 µm, smooth to faintly papillose. Calyptrae mitrate, 1.5–2.0 mm long, yellowish white, irregularly lobed at base, sparsely hairy or naked.

Illustrations. Bartram (1949, Fig. 136 A–C, as *Hookeriopsis crugeriana*). Figure 221.
Habitat. On stones, wet banks, fallen tree trunks, and rotting logs; 1100–2430 m.
Distribution in Central America. GUATEMALA. Quetzaltenango: *Standley 65306a* (F, FH). COSTA RICA. Guanacaste: *Chávez 300*, *307*, *Dauphin & Valdelomar 2437* (all MO).
World range: Central America.

Thamniopsis oedodontia is medium-sized species with erect to erect-spreading, ovate-lanceolate leaves that are somewhat crispate to lightly undulate when dry. Its leaves are monomorphic, elimbate, with massive, swollen, often bifid teeth on the margins, very long linear-flexuose leaf cells, and relatively short costae that can be strongly spinose on the back side (the teeth sometimes bifid) and stoutly project at the tips. It is the only Central American species of *Thamniopsis* that lacks a massive annulus; otherwise, the technical features of its sporophytes are identical to those of other Central American species of *Thamniopsis*, but they are distinctly smaller.

The swollen, massive, bifid marginal teeth of *T. oedodontia* are identical in form to those of *T. incurva*. Plants of *T. incurva*, however, are often reddish or purplish tinged and differ from *T. oedodontia* in having asymmetric, ovate, obovate, or oblong lateral leaves that are obtuse to broadly rounded. Furthermore, the costae of *T. incurva* are smooth at back and the upper leaf cells are broadly hexagonal to rhomboidal. In overall aspect *T. oedodontia* and *T. undata* are very similar, and both species have monomorphic leaves. *Thamniopsis undata* differs from *T. oedodontia* in having sharply serrate leaf margins (the teeth narrow and elongate) that are more or less bordered by several rows of long, narrow cells, and long-hexagonal to long-rectangular often porose leaf cells. In addition, its sporophytes are considerably larger: setae 24–40 mm long; capsules 1–3 mm long; opercula 2.0–2.5 mm long; annuli of 7–9 rows of cells; and calyptrae 2.5–3.0 mm long. *Thamniopsis cruegeriana* differs from *T. oedodontia* in having dimorphic leaves, but the acuminate leaf form of *T. cruegeriana* is very similar to that of the leaves of *T. oedodontia*. Although the acuminate leaves of *T. cruegeriana* can have swollen, bifid marginal teeth, they are never as large and swollen as those of *T. oedodontia*, and the lower margins are usually smooth. Furthermore, the leaves of *T. cruegeriana* usually have much stronger costae than those of *T. oedodontia.*

8. *Thamniopsis pendula* (Hook.) M. Fleisch., Musci Buitenzorg 3: 952. 1908. *Hookeria pendula* Hook., Musci Exot. 1: 53. 1818. *Chaetophora pendula* (Hook.) Brid., Bryol. Univ. 2: 338. 1827. *Hookeriopsis pendula* (Hook.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 364. 1877. Protologue. Regione temperata in jugis Andium, *Humboldt et Bonpland*. Types. *Hookeria pendula*, *Humboldt 97*, Hook. M. Exot. t. 53, [Herbarium Hookerianum] (BM, lectotype, designated here); In jugis Andium regione temperata truncicola, leg. *Humboldt & Bonpland* [Herb. Hampe] (BM, isolectotype); "Regione temperata in jugis Andium," *No. 96*, same *97 nov. sp* [Herbarium Hookerianum] (BM, syntype).

Cyclodictyon maxoni R. S. Williams, Contr. U.S. Natl. Herb. 16: 24. 1912. Protologue. [Panama] Humid forest along the upper Caldera River, near "Camp I," Holcomb's trail, above El Boquete, Chiriqui, altitude 1450 to 1650 meters, March 22 to 24, 1911, *Maxon 5619*. Types. Panama. Humid forest along the upper Caldera River, near "Camp I," Holcomb's trail, above El Boquete, Chiriqui; altitude 1450 to 1650 meters, March 22 to 24, 1911, *Maxon 5619* (US, holotype; NY, isotype), *syn. nov*.

Plants robust, 6–12 cm long, greenish, yellowish green, to reddish yellow, in dense mats. Stems prostrate or erect-ascending, at times becoming subdendroid, frondose, irregularly pinnately to bipinnately branched, hyaline to yellowish when young, becoming reddish with age, subcomplanate-foliate; stems in cross section with hyalodermis, subepidermis of 2–3 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia small, foliose; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves somewhat flattened, imbricate or erect-spreading, smooth, somewhat flaccid when dry, erect-spreading when wet, monomorphic, ovate, oblong-ovate to oblong-ligulate, stem leaves 1.6–2.0 mm long, branch leaves 1.1–1.7 mm long, symmetric, gradually narrowed to rounded or obtuse, often apiculate apices, plane to weakly concave; margins entire below, entire to subentire at apices, plane below, broadly incurved above, elimbate; costae double, ending 2/3–3/4 the leaf length, more or less diverging throughout, usually unequal, smooth at back, at times weakly projecting at the tips; cells smooth, upper cells elongate-hexagonal to elongate-flexuose, 20–50 × 4–6 µm, firm-walled, usually porose, median and basal cells linear-flexuose, 32–70 × 4 µm, thick-walled, porose; basal cells along the insertions oblong-rectangular to long-rectangular, porose; alar cells not differentiated. Dioicous. Setae elongate, 30–45 mm long, red, smooth throughout, at times somewhat roughened below the capsules. Capsules horizontal to pendent, oblong-cylindric, 2–3 mm long, neck well developed; exothecial cells quadrate in 2–4 rows at mouth, those below oblong to rectangular, lateral walls evenly thickened, horizontal walls collenchymatous; stomata rudimentary, 3–4-celled, on neck; opercula long conic-rostrate, 1.5–2.0 mm long; annuli of 7–9 rows of transversely rectangular, thin-walled cells, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome narrowly triangular with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface dark red, densely and closely cross-striate below, coarsely papillose above, primary walls yellow, smooth, ventral (inner) surface hyaline to yellowish, deposition thin, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not or faintly perforate, cilia absent. Spores rounded, 10–18 µm, smooth to faintly papillose. Calyptrae mitrate, 3–4 mm long, yellowish white, irregularly lobed at base, sparsely hairy.

Illustrations. Hooker (1818, Pl. 53); Brotherus (1907a, Fig. 686); Brotherus (1925, Fig. 612); Welch (1974, Figs. 454–464); Churchill and Linares (1995, Fig. 45 e–i); Vaz and Costa (2006b, Figs. 116–122). Figure 222.

Habitat. On rocks, boulders, tree trunks, and logs in or near streams, and on rotting sticks; 1200–2100 m.

Distribution in Central America. COSTA RICA. Cartago: *Crosby & Crosby 5760* (MO); Heredia: *Skutch 3185* (FH, MO, NY, US); Puntarenas: *Dauphin 1477* (MO); San José: *Griffin & Morales A16* (F, FH, MO, NY, US). PANAMA. Bocas del Toro: *Allen 5046* (MO); Chiriquí: *McPherson 6825C* (MO); Darién: *Mori & Gentry 4506* (MO); Veraguas: *Crosby 10197* (MO).

World range: Central America; Western South America, Brazil.

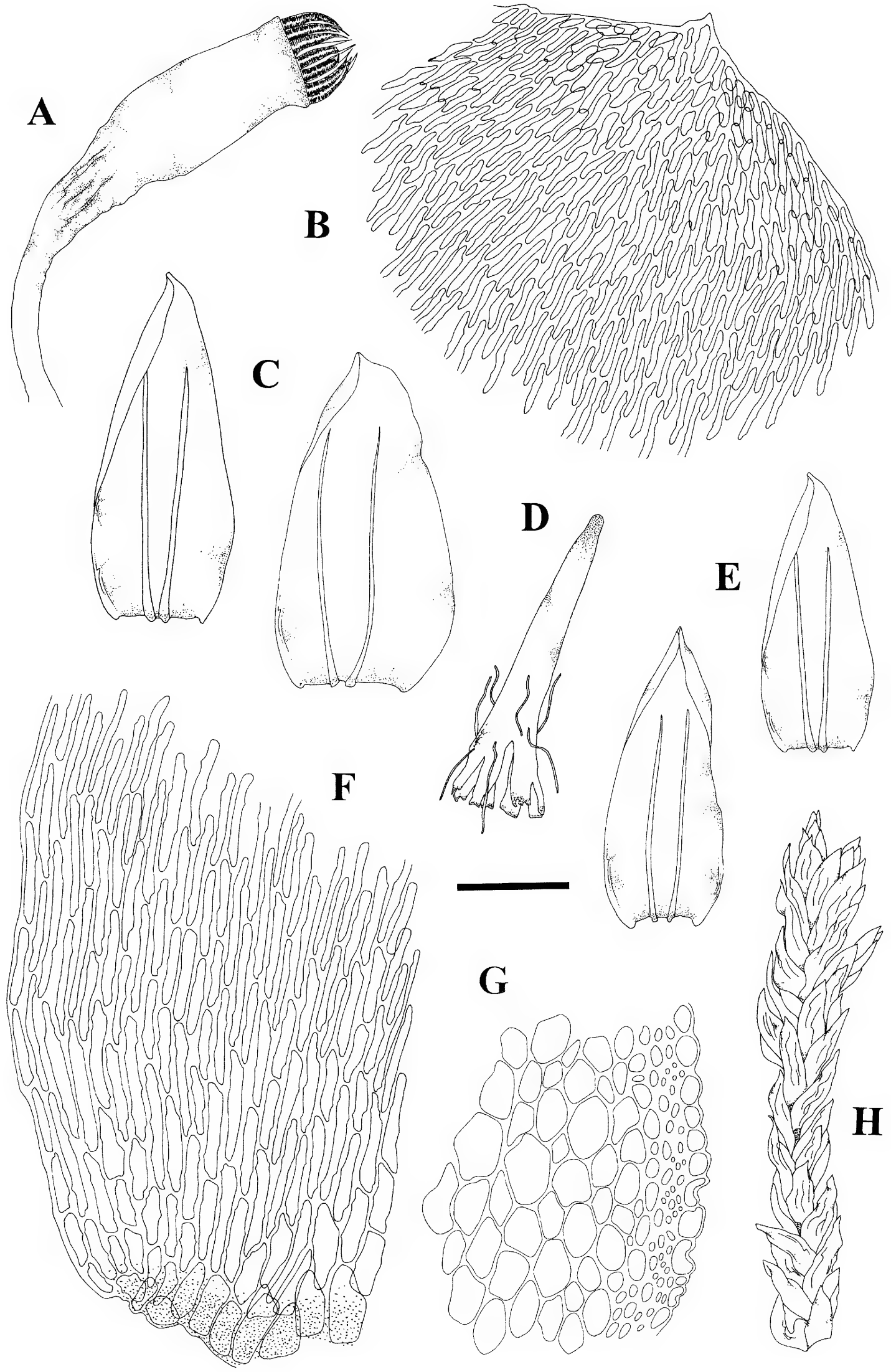
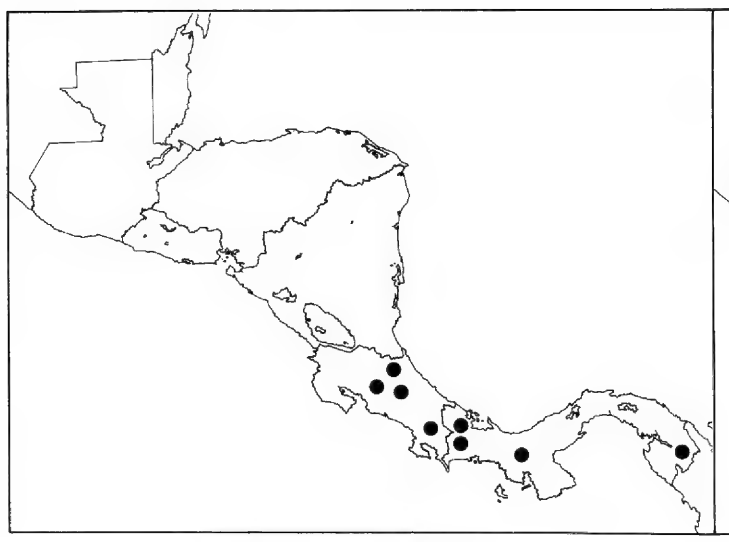
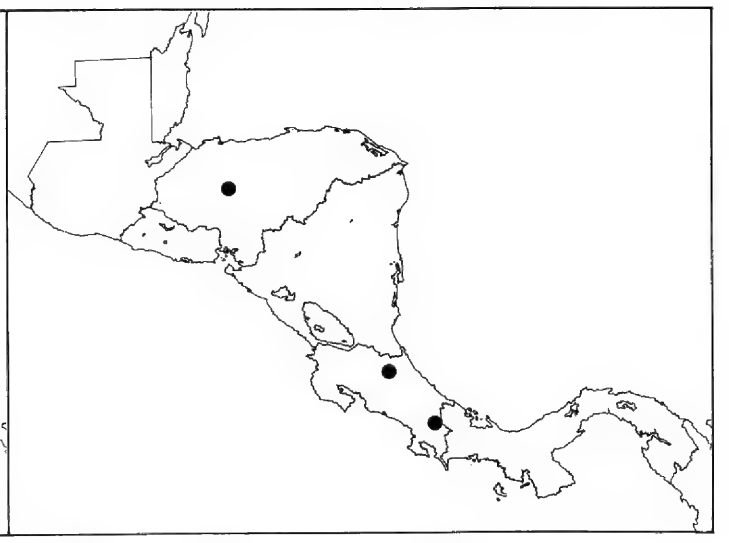


Figure 222. *Thamniopsis pendula*. A. Seta and capsule. B. Leaf apex. C. Stem leaves. D. Calyptra. E. Branch leaves. F. Basal and alar cells. G. Stem in cross section. H. Habit. Scale in mm: bar = 0.06 (B, F); bar = 0.13 (G); bar = 0.6 (C, E); bar = 1.25 (A, D); bar = 1.96 (H). A from *Skutch 3185*; D from *Crosby 5805*; F, G from *Crosby 18846*; all other figure parts from *Crosby 5760*.



Thamniopsis pendula



Thamniopsis purpureophylla

Thamniopsis pendula is a robust species known in Central America only from Costa Rica and Panama. The species typically grows on wet rocks in or along streams; occasionally it occurs on logs or tree trunks. The stems of *T. pendula* are erect-ascending and irregularly pinnate to bipinnately branched. Although they are sometimes described as dendroid, they are closer to frondose because the branches are more or less in one plane. *Thamniopsis pendula* has monomorphic, ovate, oblong-ovate to oblong-ligulate leaves that are erect to erect-spreading and somewhat complanate when wet. When dry the leaves are stiffly erect but wavily contorted in such a way that they appear to be flaccid. Its gradually rounded to obtuse leaves have entire or subentire margins that are elimbate, and have long, flexuose cells that are thick-walled and porose throughout in the same way as species of *Brymela*. The costae in *T. pendula* are smooth at back and occasionally project slightly at the tips. The sporophyte of *T. pendula* is typical for the genus: very long setae; pendent, cylindrical capsules; long rostrate opercula; large, massive 7–9-celled annulus persistent on the operculum; and perfect hookeriaceous peristome. The calyptrae are large, mitrate, irregularly lobed at base, and often sparsely hairy.

There is no other Central American species of *Thamniopsis* comparable to *T. pendula* because of its monomorphic, broadly rounded to obtuse, ovate to oblong-ovate leaves with entire margins. Nevertheless, the species can be confused with some expressions of *T. cruegeriana* or *T. diffusa*. These species have dimorphic leaves: lanceolate with slenderly acute apices, strongly serrate margins, and costae serrate-crested on the back side; and broadly rounded to obtuse, ovate to oblong-ovate with entire margins. For the most part, there is little problem separating these species from *T. pendula* because the lanceolate-type leaves usually predominate in the collections. However, there are collections of *T. cruegeriana* and *T. diffusa* that consist nearly entirely of broadly rounded to obtuse, ovate to oblong-ovate leaves. Distinguishing these collections from *T. pendula* often depends on finding at least some lanceolate leaves. Nevertheless, even in the complete absence of lanceolate leaves, these species can be separated from *T. pendula* by their smaller size (stem leaves 1.0–1.7 mm vs. 1.6–2.0 mm long). Furthermore, the broadly rounded to obtuse, ovate to oblong-ovate leaves in *T. cruegeriana* and *T. diffusa* often have some leaves with costae that are serrate-crested at back and have multicellular projections at the tips.

There are three elements at BM that appear to be type material. One is from the Hampe Herbarium; it represents an isolectotype. The other two are from the Hooker herbarium and have different collection numbers (*97* and *96*). The label information for specimen no. *96* agrees closely with the Protologue, "'Regione temperata in jugis Andium,' *No. 96*, same *97 nov. sp.*," while the other contains only the information "*Humboldt 97*, Hook. M. Exot. t. 53." The second specimen is chosen as the lectotype because the specimen agrees more closely with Hooker's original illustration. There are two collections of the isotype of *Cyclodictyon maxoni* (*Maxon 5619*) at NY. One of these collections is *Thamniopsis pendula*; the other is *Lepidopilum tortifolium*.

9. *Thamniopsis purpureophylla* (Müll. Hal. *ex* E. Britton) W. R. Buck, Brittonia 39: 219. 1987.

Hookeria purpureophylla Müll. Hal. *ex* E. Britton, Bull. Torrey Bot. Club 23: 492. 1896. Proto-

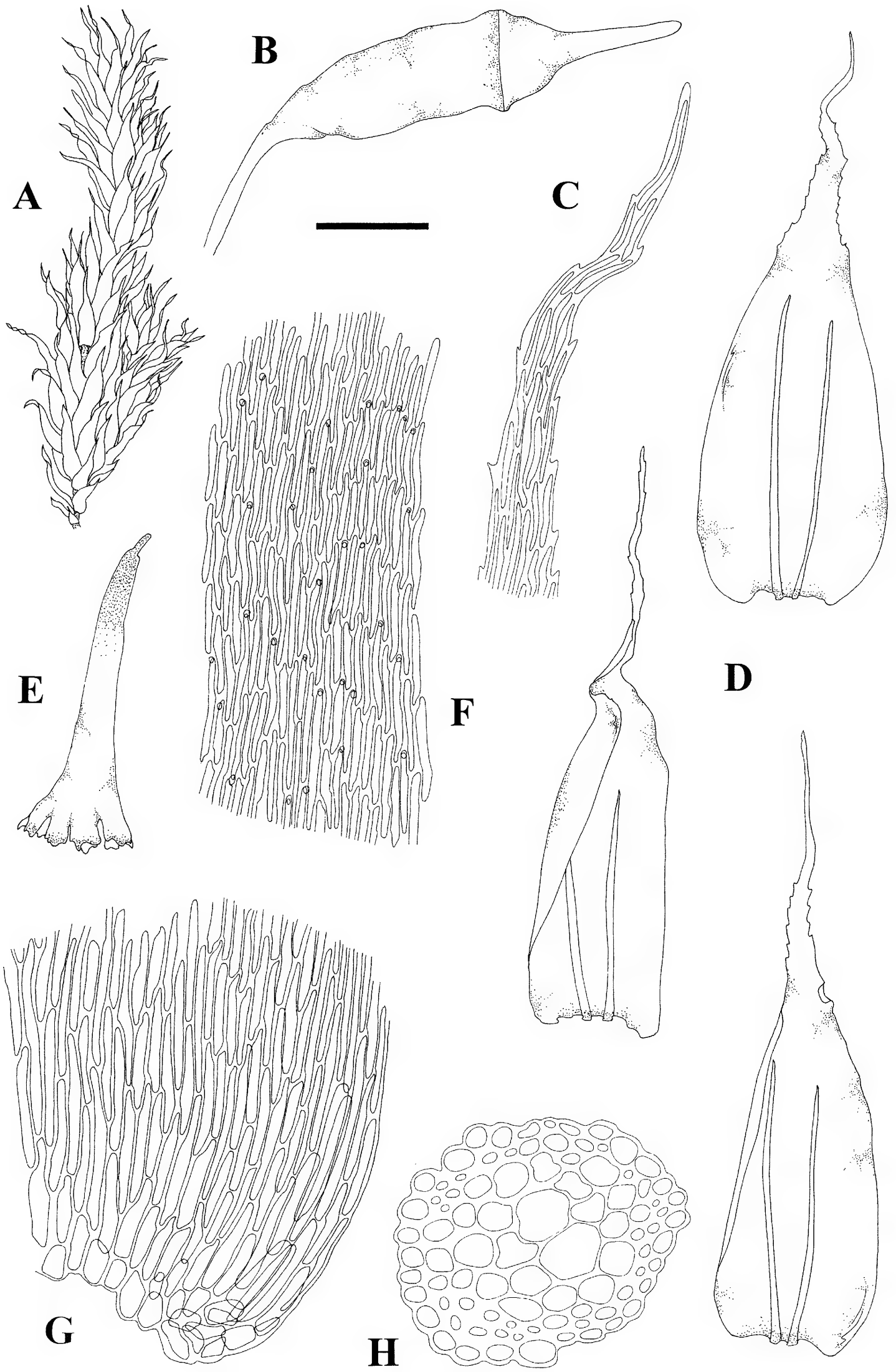


Figure 223. *Thamniopsis purpureophylla*. A. Habit. B. Seta, capsule, and operculum. C. Leaf apex. D. Leaves. E. Calyptra. F. Upper leaf cells. G. Basal and alar cells. H. Stem in cross section. Scale in mm: bar = 0.06 (C, F, G); bar = 0.08 (H); bar = 0.7 (B, D, E); bar = 1.56 (A). All figure parts from *Crosby 6055*.

logue. [Bolivia] Near Yungas, 6000 ft., 1885, [*Rusby*] *3164*. Type. Near Yungas, Bolivia. 6000 ft., 1885, *H. H. Rusby 3164* (NY, holotype).

Plants slender, 1–2 cm long, reddish to purple tinged, in thin mats. Stems prostrate, irregularly to subpinnately branched, hyaline to yellowish when young, becoming red with age, evenly foliate; stems in cross section with hyalodermis, subepidermal layer of 2–3 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia small, foliose; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect to erect-patent, flexuose-contorted, lightly undulate when dry, erect-spreading when wet, monomorphic, oblong-lanceolate to ovate-lanceolate, 1.0–1.5 mm long, symmetric, abruptly constricted at base of acumina, concave; margins serrate to serrulate in upper 2/3, subentire below, plane to erect, not bordered; costae double, thin, ending 2/3 the leaf length, diverging throughout, usually unequal, smooth at back, occasionally projecting at the apices; cells smooth or prorate, upper cells linear-elongate, 20–70 × 3–5 µm, firm-walled, at times porose, lower cells oblong-rectangular to long-rectangular, porose, bulging near insertions, cells across the insertions reddish, short-rectangular, porose; alar cells not differentiated. Autoicous. Setae elongate, 15–20 mm long, red, flexuose, smooth below, lightly roughened below the capsules. Capsules inclined, short-cylindric, 1.0–1.5 mm long, neck well developed; exothecial cells quadrate to oblate in 2–3 rows at mouth, those below oblong to rectangular, collenchymatous; stomata rudimentary, 3–4-celled, on neck; opercula conic-rostrate, 1.0–1.5 mm long; annuli of 7–9 rows of quadrate cells, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome narrowly triangular with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface yellow brown, densely and closely cross-striate below, coarsely papillose above, primary walls yellowish to hyaline, smooth, ventral (inner) surface hyaline to yellowish, deposition thin, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not perforate, cilia absent. Spores rounded, 8–12 µm, smooth to faintly roughened. Calyptrae mitrate, 2.0 mm long, yellowish below, reddish above, irregularly lobed at base, naked.

Illustrations. Churchill and Linares (1995, Fig. 46 a–c). Figure 223.

Habitat. On tree roots and twigs; 1760–2100 m.

Distribution in Central America. HONDURAS. Comayagua: *Allen 13928* (MO). COSTA RICA. Heredia: *Crosby & Crosby 6055* (MO); Puntarenas: *Gómez 20041A* (MO).

World range: Central America; Western South America.

Thamniopsis purpureophylla is a slender species with evenly foliate stems and reddish to purplish tinged leaves that are erect-patent and undulate when dry. Its ovate- to oblong-lanceolate leaves are usually abruptly constricted above to long, slender acumina. This last feature of the species is best seen at the ends of the stems and branches where the clustered leaves form enlarged buds. The upper leaf margins in *T. purpureophylla* vary from sharply serrate to serrulate; the narrowly linear upper leaf cells are smooth or prorate and the basal cells are enlarged and variously rectangular.

The presence of monomorphic leaves that are constricted at the base of the acumina separates *T. purpureophylla* from all other Central American species except the *acicularis*-form of *T. undata*, *T. steyermarkii*, and *T. glandulifera*. The *acicularis*-form of *T. undata* differs from *T. purpureophylla* in having more strongly undulate, considerably larger leaves (2.5–4.0 mm vs. 1.0–1.5 mm long), broader upper leaf cells (3–14 µm vs. 2–4 µm wide), and somewhat swollen marginal teeth. *Thamniopsis steyermarkii*, *T. glandulifera*, and *T. purpureophylla* are nearly identical in size, leaf shape, and cell form. *Thamniopsis glandulifera* differs from *T. purpureophylla* in its yellowish green color and in having high, spiculose-papillose leaf cells. *Thamniopsis steyermarkii* differs from *T. purpureophylla* in having a green or yellowish color and consistently smooth upper leaf cells.

The species of *Stenodictyon* and *Thamniopsis purpureophylla* are similar in having leaves that are abruptly constricted above to long, slender acumina. Furthermore, some *Stenodictyon* species are identical in size and aspect to *T. purpureophylla*. *Stenodictyon* differs from *T. purpureophylla* in having entire leaf margins and smooth leaf cells.

10. *Thamniopsis rivularis* (Mitt.) B. H. Allen, *comb. nov.* Basionym: *Hookeria rivularis* Mitt., J. Linn. Soc., Bot. 12: 353. 1869. *Callicostella rivularis* (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 355. 1877. *Schizomitrium rivulare* (Mitt.) H. A. Crum, Bryologist 87: 208. 1984. Protologue. [Ecuador] Andes Quitenses, fl. Bombonasa in rivulis (1500 ped.), *Spruce, n. 668*. [Peru] Andes Peruvianae, Tavalosos, ad saxa rivulorum (2500 ped.), *Spruce, n. 669*. Types. Bombonasa, *Spruce 688* (NY, syntype); Tavalosos, ad saxa rivolorum, 2500 ped., [*Spruce*] *669* (NY, syntype).

Hookeria filescens Schimp. *ex* Besch., Ann. Sci. Nat., Bot. sér. 4, 3: 235. 1876. *Callicostella filescens* (Schimp. *ex* Besch.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 354. 1877. Protologue. Guadeloupe (*L'Herminier, n° 45 ex parte*).

Hookeria hospitans Schimp. *ex* Besch., Ann. Sci. Nat., Bot. sér. 4, 3: 236. 1876. *Hookeriopsis hospitans* (Schimp. *ex* Besch.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 361. 1877. Protologue. Guadeloupe et Martinique, sur les feuilles mortes (in herb. Schimp.).

Hookeria subfissidentoides Schimp. *ex* Besch., Ann. Sci. Nat., Bot. sér. 4, 3: 235. 1876. *Hookeriopsis subfissidentoides* (Schimp. *ex* Besch.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 361. 1877. *Callicostella subfissidentoides* (Schimp. *ex* Besch.) Broth., Nat. Pflanzenfam. I(3): 937. 1907. *Schizomitrium subfissidentoides* (Schimp. *ex* Besch.) H. A. Crum, Bryologist 87: 208. 1984. Protologue. Guadeloupe (*L'Herminier*, in herb. Schimp.).

Plants slender, 1–4 cm long, green or reddish yellow, in dense or loose mats. Stems prostrate, irregularly branched, hyaline to yellowish when young, becoming reddish with age; stems in cross section with moderate-sized hyalodermis, subepidermis of 2–3 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent, foliose scale leaves present; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown to blackish brown, not or sparsely and irregularly branched. Leaves erect to erect-spreading, slightly flexuose when dry, erect-spreading when wet, oblong-ovate to ovate-lanceolate, 0.6–1.5 mm long, acute to broadly short-acuminate; margins serrate to serrulate in upper 2/3, teeth single, not swollen, entire below, plane, lateral leaves often with lower margin broadly inflexed on one side; costae double, weak, ending 2/3–3/4 the leaf length, diverging throughout, unequal, smooth on back, at times weakly projecting at the apices; cells smooth, upper cells oval-hexagonal to long-rhomboidal, 14–34 × 5–10 µm, firm-walled, eporose, lower cells elongate-rhomboidal to long-rectangular; basal cells near the insertion enlarged, oblong-rectangular; alar cells not differentiated. Dioicous. Setae elongate, 7–10 mm long, red to orange, flexuose, papillose throughout. Capsules suberect to horizontal, short-cylindric, 1.0 mm long, neck well developed; exothecial cells quadrate to oblate in 2–4 rows at mouth, those below oblong to rectangular, lateral walls evenly thickened, horizontal walls collenchymatous; stomata rudimentary, on neck; opercula conic-rostrate, 0.5–0.7 mm long; annuli of 7–9 rows of cells, lower cells transversely rectangular, upper cells quadrate, all cells thin-walled with irregular nodose thickenings, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome narrowly triangular with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface dark red, densely and closely cross-striate below, coarsely papillose above, primary walls yellow, smooth, ventral (inner) surface hyaline to yellowish, deposition thin, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not or faintly perforate, cilia absent. Spores rounded, 8–12 µm, smooth to faintly roughened. Calyptrae mitrate, 1 mm long, yellowish white, red above, irregularly lobed at base, smooth.

Illustrations. Welch (1971b, Figs. 48–58, Figs. 59–71); Churchill and Linares (1995, Fig. 36 a–d); Buck (1998, Pl. 24 1–11). Figure 224.

Habitat. On rocks or boulders in and along streams, occasionally on wet rocks along trails; near sea level to 730 m.

Distribution in Central America. BELIZE. Toledo: *Allen 18717A* (MO). GUATEMALA. Izabal: *Steyermark 41779* (F, FH, NY). HONDURAS. Atlántida: *Standley 54844* (F, FH, US); Yoro: *Allen*

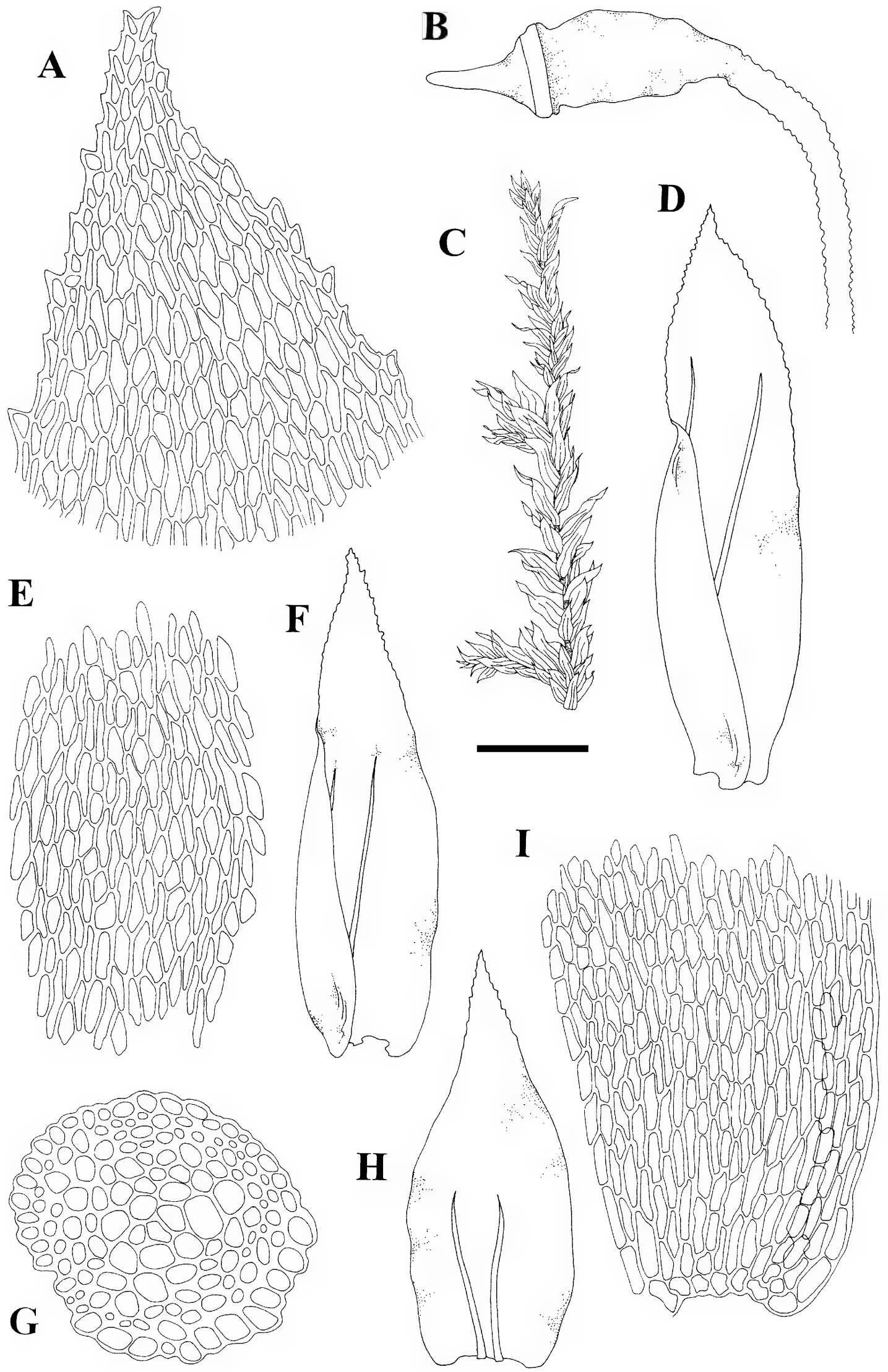
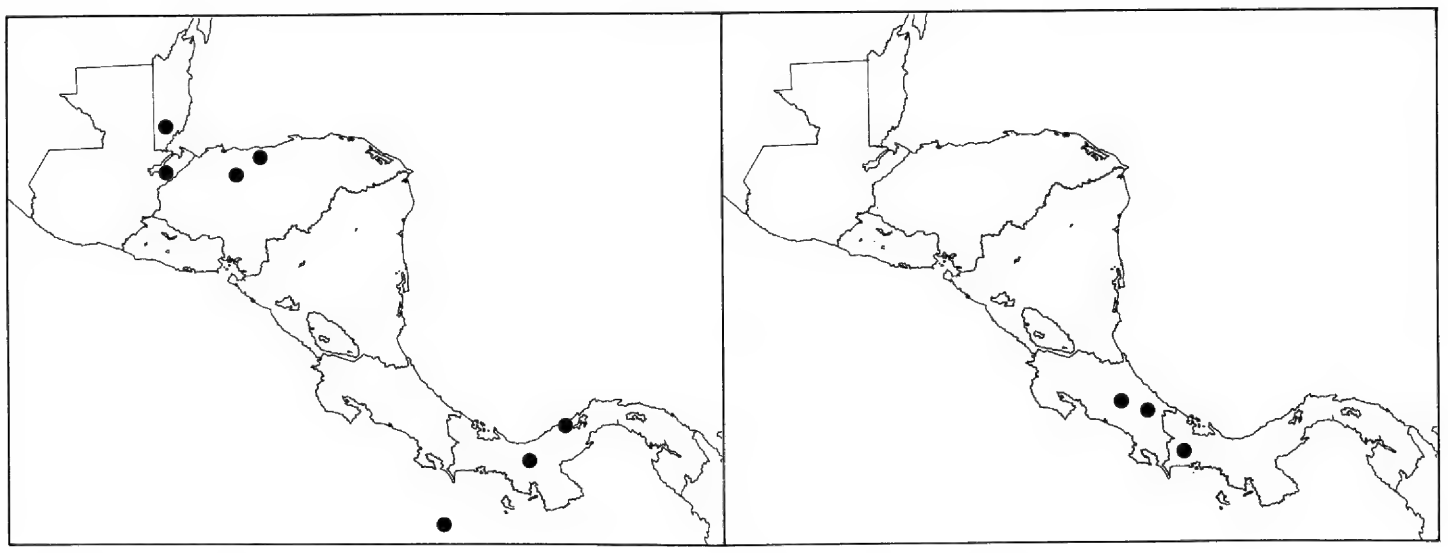


Figure 224. *Thamniopsis rivularis*. A. Leaf apex. B. Seta, capsule, annulus, and operculum. C. Habit. D & F. Lateral leaves. E. Median leaf cells. G. Stem in cross section. H. Dorsal leaf. I. Basal and alar cells. Scale in mm: bar = 0.06 (A, E, G, I); bar = 0.28 (D, F, H); bar = 0.5 (B); bar = 1.96 (C). B from *Standley 54844*; C from *Crosby 10236*; all other figure parts from *Spruce 669* (syntype).



Thamniopsis rivularis *Thamniopsis standleyi*

13499 (MO). COSTA RICA. Puntarenas: Cocos Island, *Gómez 4607* (CR, MO). PANAMA. Colón: *Crosby 10764* (MO); Veraguas: *Crosby 10236* (MO, PMA).

World range: Central America; Caribbean; Western South America.

Thamniopsis rivularis is a small species that nearly always grows on rocks in and along streams. The species has stems with a weakly developed, but distinct hyalodermis; short, oblong-ovate to ovate-lanceolate leaves with acute to broadly acuminate apices; obscurely bordered upper leaf margins with non-swollen, single teeth that more or less alternate from serrulate to serrate; oval-hexagonal to rhomboidal-hexagonal upper leaf cells; and weak, smooth costae that are unequal in length and only occasionally project at the tips. *Thamniopsis rivularis* is dioicous. Its setae are scabrous throughout, but otherwise the sporophytes are typical for *Thamniopsis.*

Thamniopsis rivularis is usually placed in *Callicostella*, but it differs from that genus in having a stem hyalodermis, and most but not all species of *Callicostella* have papillose leaf cells. When treated within *Callicostella* it typically has been associated with *C. colombica* and *C. guatemalensis*; all three species are here positioned in *Thamniopsis.* These three species differ from all other Central American species of *Thamniopsis* in their oval-hexagonal to rhomboidal-hexagonal upper leaf cells and small, slender size: plants mostly 1 cm long; leaves often less than 1.2 mm; setae 4–15 mm long; capsules 0.5–1.5 mm long; and calyptrae 1.0–1.5 mm long. *Thamniopsis colombica* is also similar to *T. rivularis* in its dioicous sexual condition and in having setae that are scabrous throughout. It differs from *T. rivularis* in having much wider upper leaf cells (10–20 µm vs. 5–10 µm) and leaves that lack any trace of a leaf border. *Thamniopsis guatemalensis* differs from *T. rivularis* only in having swollen, often bifid teeth on the upper leaf margins, an autoicous sexual condition, and smooth setae.

Among the smooth-celled species of *Callicostella*, *Thamniopsis rivularis* is most similar to *C. merkelii* in size, leaf shape, and leaf cell form. *Callicostella merkelii* differs from *T. rivularis* in having a stem sclerodermis, distinctive, foliose pseudoparaphyllia, and leaves with stout costae that usually strongly converge at the tips.

11. *Thamniopsis standleyi* (E. B. Bartram) B. H. Allen, *comb. nov.* Basionym: *Hookeriopsis standleyi* E. B. Bartram, Contr. U.S. Natl. Herb. 26: 102. 1928. Protologue. On tree, vicinity of Pejivalle, Province of Cartago, Costa Rica, altitude about 900 meters, *Paul C. Standley* and *Juvenal Valerio*, February 7 and 8, 1926, *no. 47155*. Types. Costa Rica. On tree, vicinity of Pejivalle, Provincia de Cartago, Costa Rica, altitude about 900 meters, *Paul C. Standley & Juvenal Valerio, No. 47155* Febr. 7–8, 1926 (US, holotype; FH, NY, isotypes).

Plants small and slender, 1–2 cm long, green or yellowish red, in dense mats. Stems prostrate, irregularly branched, yellowish when young, red with age; stems in cross section with hyalodermis of one row of cells, subepidermis of 1–3 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia subfoliose; axillary hairs 2-celled,

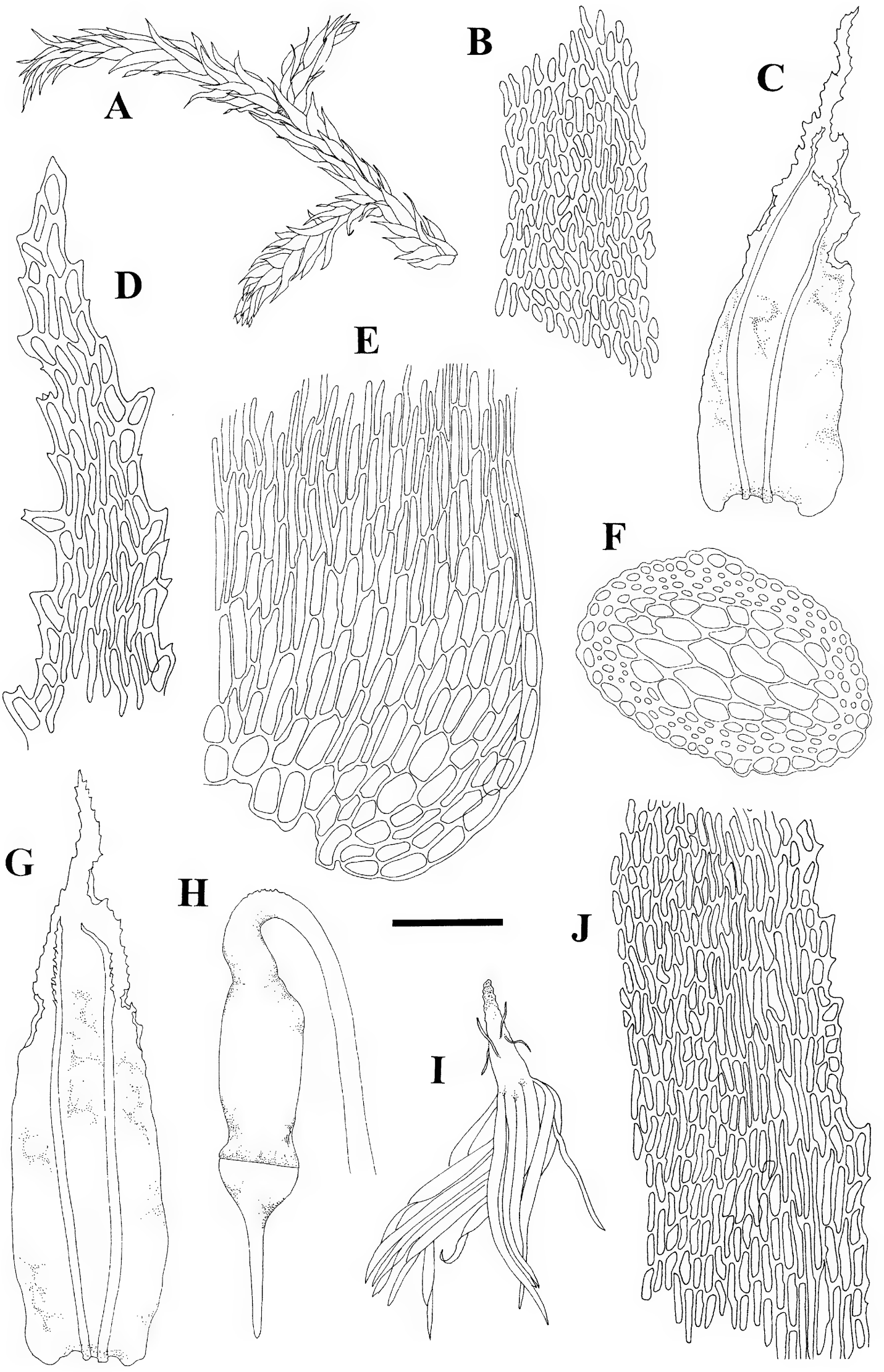


Figure 225. *Thamniopsis standleyi*. A. Habit. B. Upper leaf cells between the costae. C & G. Leaves. D. Leaf apex. E. Basal and alar cells. F. Stem in cross section. H. Seta, capsule, and operculum. I. Calyptra. J. Upper leaf cells and margin showing intramarginal border. Scale in mm: bar = 0.05 (B, D, J); bar = 0.06 (E); bar = 0.08 (F); bar = 0.28 (C, G); bar = 0.9 (H); bar = 1.56 (I); bar = 1.96 (A). H from *Folsom 67*; all other figure parts from *Alfaro 67*.

basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect, crispate and transversely undulate above when dry, erect-spreading when wet. Dorsal and lateral leaves lanceolate to oblong-ovate, 1.0–1.5 mm long, gradually acuminate; margins coarsely serrate to dentate in upper 2/3, teeth single or bifid, at times multicellular, serrulate to entire below, plane below, undulate and irregularly recurved to erect above, often with intramarginal border of narrow, elongate cells; costae double, ending 2/3–3/4 the leaf length, serrate to dentate on back, strongly projecting at apices; cells smooth or prorate in upper 2/3, upper and median cells long-rectangular to linear-flexuose, 8–20 × 2–4 μm, eporose or porose, firm- to thick-walled; basal cells linear, those near insertions enlarged, firm or bulging, oblong-rectangular; alar cells not differentiated. Ventral leaves erect, lanceolate to ovate-lanceolate, upper and median cells elongate; basal cells long-rectangular, more or less differentiated from the upper and median cells. Dioicous (?), male plants not seen, perichaetia lateral on stems and branches. Setae elongate, 15–25 mm long, red, flexuose, smooth below, somewhat roughened to lightly scabrose below capsules. Capsules inclined to pendent, short-cylindric, 1.0–1.5 mm long, neck well developed; exothecial cells quadrate to oblate in 2–3 rows at mouth, those below oblong to rectangular, collenchymatous; stomata rudimentary, 3–4-celled, on neck; opercula conic-rostrate, 1.5 mm long; annuli of 7–15 rows of quadrate cells, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome narrowly triangular with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface yellow, densely and closely cross-striate below, coarsely papillose above, primary walls yellowish hyaline, smooth, ventral (inner) surface hyaline to yellowish, deposition thin, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not perforate, cilia absent. Spores rounded, 8–12 μm, smooth to faintly roughened. Calyptrae mitrate-laciniate, 3–4 mm long, yellowish brown, smooth below, papillose-scabrose above, sparsely hairy.

Illustrations. Bartram (1928a, Fig. 32 A–E); Welch (1974, Figs. 235–247). Figure 225.
Habitat. On trees and rotting logs; 50–1600 m.
Distribution in Central America. COSTA RICA. Cartago: *Standley & Valerio 47155* (FH, NY, US); Limón: *Alfaro 67* (F, FH). PANAMA. Chiriquí: *Folsom et al. 5328* (MO).
World range: Central America.

Thamniopsis standleyi is a slender species with lanceolate to oblong-ovate leaves that have undulate and irregularly recurved upper margins. The margins are also coarsely serrate to dentate, with teeth that can be single or bifid, and sometimes multicellular. The costae in *T. standleyi* are dentate to crested at back and strongly project at the tips. As is typical for the genus the leaves and many of the leaf characters are extremely variable. Dorsal and lateral leaves are narrow and usually have relatively short, irregularly shaped, often prorate upper and median leaf cells, while the ventral leaves are broader and typically have elongate, smooth cells throughout. The form of the basal leaf cells also varies considerably, with some leaves having narrow, elongate, porose basal cells while others have enlarged, long-rectangular, firm-walled cells. At times, the lateral and dorsal leaves have a faint intramarginal border of narrow, elongate cells. An outstanding feature of the species is found in its mitrate calyptrae, which are laciniate at base with long, narrow fimbriations. The calyptrae in *T. standleyi* are identical in form to the typical calyptrae found in *Macromitrium*. It is the only Central American *Thamniopsis* with this feature.

In Central America *Thamniopsis standleyi* is similar to *T. diffusa* in having some leaves with intramarginal borders of elongate, narrow cells. However, the smaller size of *T. standleyi* separates it from all Central American species of *Thamniopsis* except *T. colombica* and *T. guatemalensis*. *Thamniopsis colombica* differs from *T. standleyi* in having broader (10–20 μm vs. 2–4 μm wide) isodiametric, hexagonal to long-rhomboidal, thin-walled upper leaf cells. *Thamniopsis guatemalensis* has somewhat smaller leaves than *T. standleyi* (0.9–1.2 mm vs. 1.0–1.5 mm long) that are smooth rather than undulate. Typically the leaves of *T. guatemalensis* are broader (acute to short-acuminate, oblong-ovate to oblong-lanceolate vs. long-acuminate, lanceolate to oblong-ovate) than those of *T. standleyi*, and they have plane or erect upper margins with unicellular, somewhat swollen teeth. In addition, the

upper leaf cells of *T. guatemalensis* are smooth rather than prorate, wider (5–10 µm vs. 2–4 µm) than those of *T. standleyi*, and the costae are smooth to serrate at back rather than dentate to crested.

Bartram (1928a) compared *Thamniopsis standleyi* (in *Hookeriopsis*) to *Hookeriopsis rugulosa* (Mitt.) A. Jaeger, and indeed the two are remarkably similar in overall aspect. Furthermore, both species have mitrate-laciniate calyptrae. *Hookeriopsis rugulosa* is a bigger species than *Thamniopsis standleyi*, with broadly acute to obtuse leaves over 2 mm long, elongate, porose, basal leaf cells, and stems that have a sclerodermis. Buck (1987) transferred *H. rugulosa* to *Brymela*, where it fits uncomfortably due to its costae that are serrate on back, prorate leaf cells, and leaf margins that often have bifid, somewhat swollen teeth.

12. *Thamniopsis steyermarkii* (E. B. Bartram) B. H. Allen, *comb. nov.* Basionym: *Hookeriopsis steyermarkii* E. B. Bartram, Fieldiana, Bot. 28: 5. 1951. Protologue. [Venezuela] Collected along base of east-facing high sandstone bluffs, Ptari-tepuí, state of Bolívar, alt. 2410–2450 m, Nov. 7, 1944, *Julian A. Steyermark 59942*. Types. Venezuela, State of Bolívar: Ptari-tepuí, along base of east-facing high sandstone bluffs, altitude 2410–2450 m, November 7, 1944, *Julian A. Steyermark 59942* (FH, holotype; US, isotype).

Plants medium-sized, 2–6 cm long, green, yellowish, or yellow brown, in mats. Stems prostrate, irregularly to subpinnately branched, hyaline to yellowish when young, becoming reddish with age, evenly foliate; stems in cross section with hyalodermis, subepidermis of 2–3 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia small, foliose; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect to erect-patent, flexuose-contorted, at times lightly undulate when dry, erect-spreading when wet, monomorphic, oblong- to ovate-lanceolate, 2–3 mm long, symmetric, abruptly constricted at base of acumina, concave; margins serrulate to serrate in upper 2/3, subentire below, plane to erect, not bordered; costae double, thin, ending 2/3 the leaf length, diverging throughout, usually unequal, smooth at back, occasionally projecting at the apices; cells smooth, upper cells linear-elongate, 40–90 × 3–5 µm, firm-walled, porose, lower cells oblong-rectangular to long-rectangular, porose, bulging near insertions, cells across the insertions short-rectangular, porose; alar cells not differentiated. Dioicous. Setae elongate, 25–40 mm long, red, smooth throughout, or at times somewhat roughened below the capsules. Capsules horizontal to pendent, oblong-cylindric, 1.5–2.5 mm long, neck well developed; exothecial cells quadrate in 2–4 rows at mouth, those below oblong to rectangular, lateral walls evenly thickened, horizontal walls collenchymatous; stomata rudimentary, 3–4-celled, on neck; opercula long conic-rostrate, 1.0–1.5 mm long; annulus not seen; peristome diplolepideous, exostome narrowly triangular with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface dark red, densely and closely cross-striate below, coarsely papillose above, primary walls yellow, smooth, ventral (inner) surface hyaline to yellowish, deposition thin, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not or faintly perforate, cilia absent. Spores rounded, 12–18 µm, smooth to faintly papillose. Calyptrae mitrate, 2.0 mm long, yellowish white, irregularly lobed at base.

Illustration. Figure 226.

Habitat. In shallow water at base of sandstone bluffs, on humus, muddy soil, tree trunks, rotting twigs, and logs; 600–2100 m.

Distribution in Central America. NICARAGUA. Rivas: *Nee & Téllez 28111* (HNMN, MO, NY). COSTA RICA. Cartago: *Crosby & Crosby 5825* (CR, MO); Heredia: *Crosby & Crosby 5777* (CR, FH, MO, NY); Limón: *Buck 44014* (NY); Puntarenas: *Hammel 15069* (MO). PANAMA. Bocas del Toro: *Allen 5159* (MO); Chiriquí: *Croat 68010* (MO, PMA); Panamá: *Allen 4929* (MO).

World range: Central America; Western and Northern South America.

Thamniopsis steyermarkii is a medium-sized species, with evenly foliate stems and leaves that are erect-patent, somewhat glossy, and occasionally undulate when dry. Its ovate- to oblong-lanceolate leaves are abruptly constricted above to long, slender acumina. The slender leaf acumina in this spe-

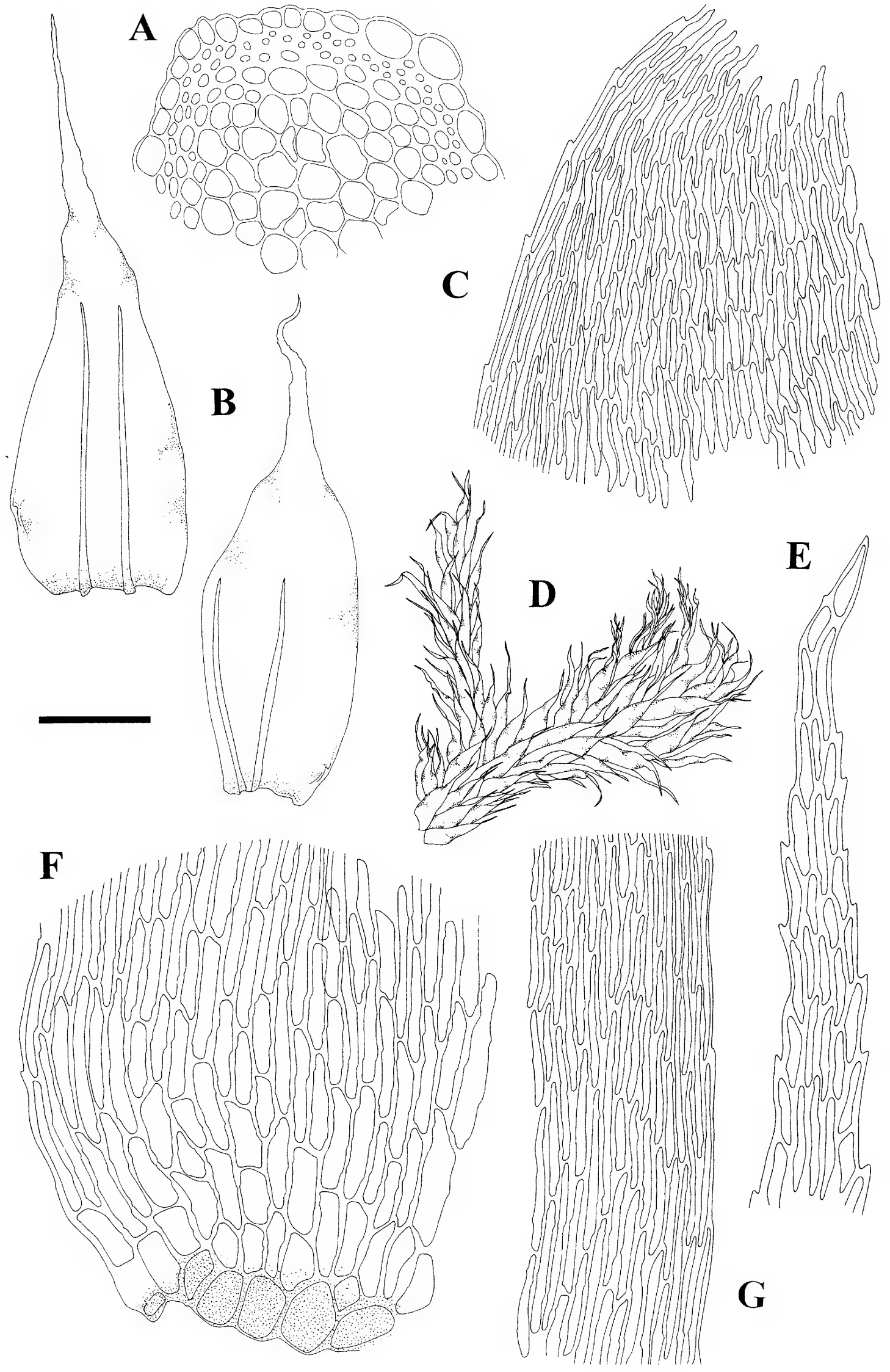
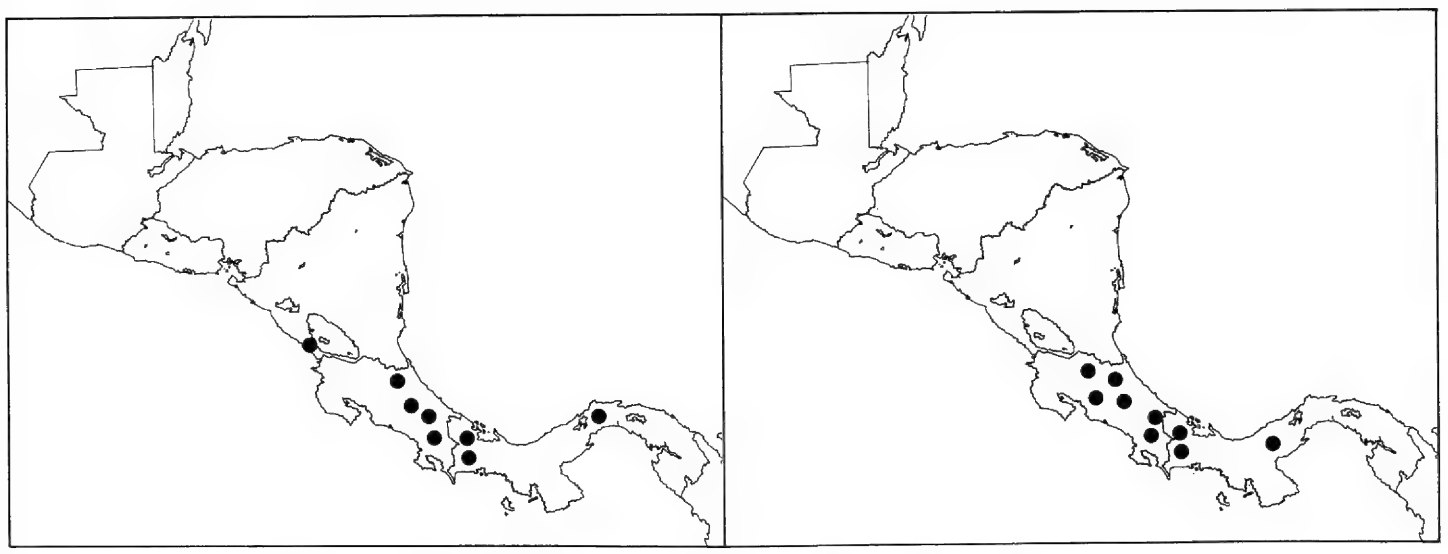


Figure 226. *Thamniopsis steyermarkii*. A. Stem in cross section. B. Leaves. C. Upper leaf cells and margin. D. Habit. E. Leaf apex. F. Basal and alar cells. G. Lower leaf cells and margin. Scale in mm: bar = 0.06 (C, E–G); bar 0.07 (A); bar = 0.5 (B); bar = 1.96 (D). All figure parts from *Allen 5159*.



Thamniopsis steyermarkii *Thamniopsis undata*

cies are especially apparent at the stem and branch tips where they are clustered in enlarged buds. The leaves have sharply serrate upper margins; smooth, porose, narrowly linear upper cells; and enlarged, variously rectangular basal cells.

The presence of monomorphic leaves that are constricted at the base of the acumina separates *T. steyermarkii* from all other Central American species of *Thamniopsis* except the *acicularis*-form of *T. undata*, *T. glandulifera*, and *T. purpureophylla.* The *acicularis*-form of *T. undata* differs from *T. steyermarkii* in having more strongly undulate leaves with broader, laxer upper leaf cells (3–14 µm vs. 2–4 µm wide) and somewhat swollen marginal teeth. *Thamniopsis purpureophylla* and *T. glandulifera* are also similar to *T. steyermarkii* in size, leaf shape, and cell form. *Thamniopsis purpureophylla* differs, however, in having a reddish purple color and distinctly prorate upper leaf cells. *Thamniopsis glandulifera* is similar to *T. steyermarkii* in color, but its leaf cells have high, spiculose papillae. *Thamniopsis steyermarkii* is uncomfortably close to *Stenodictyon*; indeed it differs from that genus only in having sharply serrate upper leaf margins.

13. *Thamniopsis undata* (Hedw.) W. R. Buck, Brittonia 39: 219. 1987. *Leskea undata* Hedw., Sp. Musc. Frond. 214. 1801. *Hypnum undatum* (Hedw.) P. Beauv., Prodr. Aethéogam. 72. 1805. *Pterygophyllum undatum* (Hedw.) Brid., Muscol. Recent. Suppl. 4: 149. 1819. *Hookeria undata* (Hedw.) Hook. & Grev., Edinburgh J. Sci. 2: 229. 1825. *Lepidopilum undatum* (Hedw.) Müll. Hal., Bot. Zeitung (Berlin) 5: 829. 1847. *Hookeriopsis undata* (Hedw.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 359. 1877. Protologue. In insula Jamaica lectam misit *D.* [sic] *Swartz.*

Hookeria crispa Müll. Hal., Bot. Zeitung (Berlin) 13: 768. 1855. *Hookeriopsis crispa* (Müll. Hal.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 358. 1877. Protologue. Venezuela, in montis nivosis provinciae Meridae et Caracas: *Moritz* 1845 misit.

Hookeria acicularis Mitt., J. Linn. Soc., Bot. 12: 354. 1869. *Hookeriopsis acicularis* (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 359. 1877. Protologue. Hab. Ins. Jamaica, *Herb. Hooker*; Guadelupe, *Parker* et ex *Herb. Sprengel*, etiam ex *Herb. Cooley* sub nom. *Hypni acicularis*, Brid.

Plants robust, 4–13 cm long, pale greenish, green, or yellowish, in dense mats. Stems prostrate, irregularly to subpinnately branched, hyaline to yellowish when young, becoming reddish with age, complanate-foliate; stems in cross section with hyalodermis, subepidermis of 2–3 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia small, foliose; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect to erect-spreading, strongly undulate and often contorted when dry, strongly undulate when wet, monomorphic, lanceolate to ovate-lanceolate, 2.5–4.0 mm long, symmetric, gradually acuminate, plane to

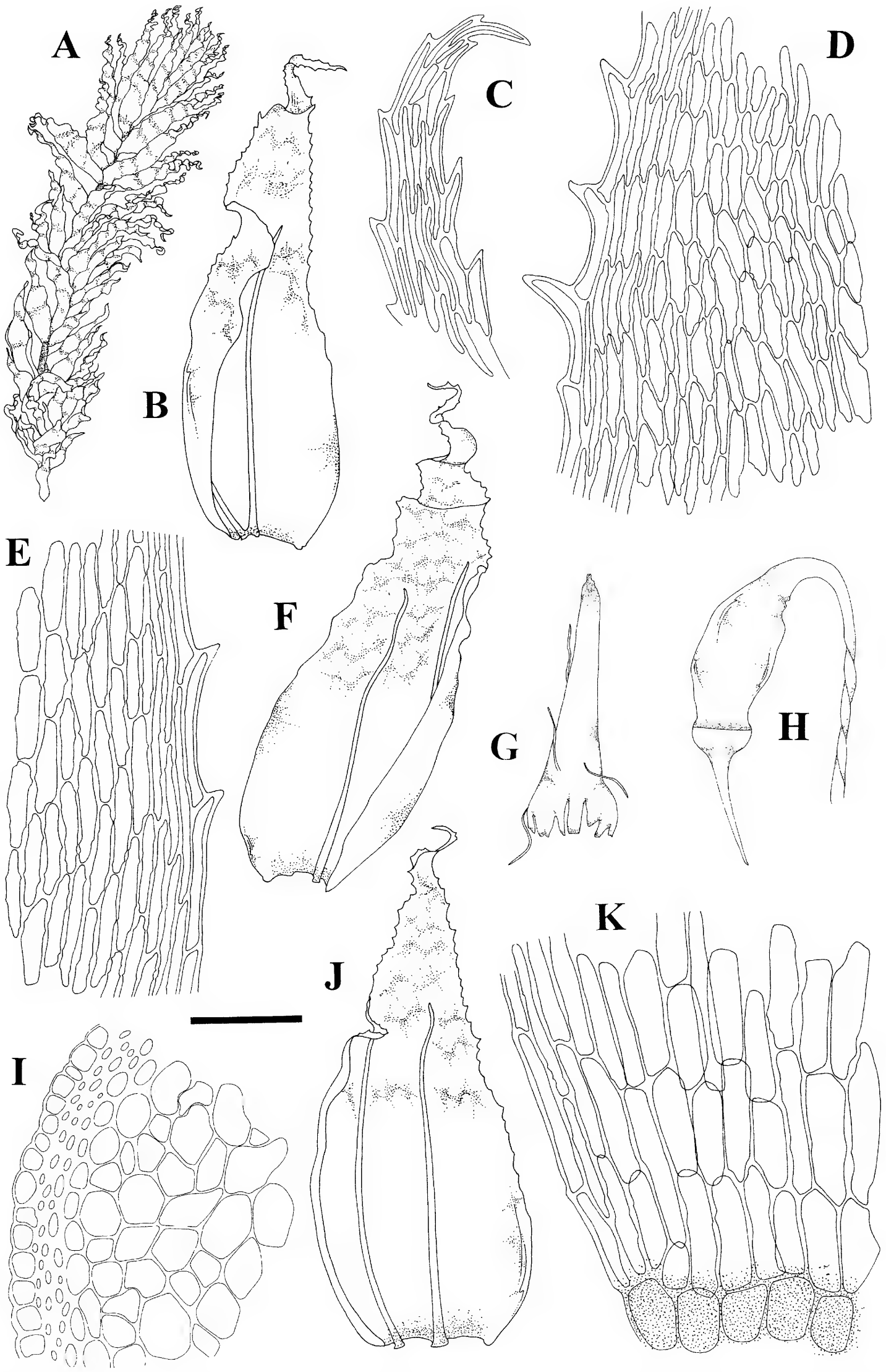


Figure 227. *Thamniopsis undata*. A. Habit. B, F & J. Leaves. C. Leaf apex. D. Upper leaf cells and margin. E. Median leaf cells and margin. G. Calyptra. H. Seta, capsule, and operculum. I. Stem in cross section. K. Basal and alar cells. Scale in mm: bar = 0.09 (C–E, K); bar = 0.13 (I); bar = 0.7 (B, F, J); bar = 1.3 (G); bar = 1.66 (H); bar = 1.96 (A). All figure parts from *Crosby 6061*.

weakly concave; margins sharply serrate in upper 2/3, subentire below, teeth long and narrow, usually broadly incurved on one side at base, otherwise plane, marginal cells narrowly elongate, forming a more or less discrete border 2–3 cells wide; costae double, thin, ending 2/3–3/4 the leaf length, diverging throughout, usually unequal, sharply toothed at back, often projecting at the apices; cells smooth, upper cells long-hexagonal, 34–90 × 3–14 μm, firm-walled, often porose, lower cells long-rectangular, thin-walled, and bulging in lower 1/3; basal cells near the insertions oblong-rectangular to long-rectangular, often porose; alar cells not differentiated. Autoicous or synoicous. Setae elongate, 24–40 mm long, red, smooth throughout, or at times somewhat roughened below the capsules. Capsules horizontal to pendent, oblong-cylindric, 1–3 mm long, neck well developed; exothecial cells quadrate in 2–4 rows at mouth, those below oblong to rectangular, lateral walls evenly thickened, horizontal walls collenchymatous; stomata rudimentary, 3–4-celled, on neck; opercula long conic-rostrate, 2.0–2.5 mm long; annuli of 7–9 rows of transversely rectangular, thin-walled cells, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome narrowly triangular, with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface dark red, densely and closely cross-striate below, coarsely papillose above, primary walls yellow, smooth, ventral (inner) surface hyaline to yellowish, deposition thin, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not or faintly perforate, cilia absent. Spores rounded, 10–14 μm, smooth to faintly papillose. Calyptrae mitrate, 2.5–3.0 mm long, yellowish white, irregularly lobed at base, sparsely hairy.

Illustrations. Welch (1969, Figs. 138–147); Welch (1971b, Figs. 130–139); Florschütz-de Waard (1986, Fig. 123); Churchill and Linares (1995, Fig. 46 h–j); Buck (1998, Pl. 8 14–21); Vaz and Costa (2006b, Figs. 131–138). Figure 227.

Habitat. On tree trunks, branches, and roots, rotting trunks, branches, and logs, terrestrial on wet, shaded banks, and wet rocks often along or in streams; (140–)600–2600 m.

Distribution in Central America. COSTA RICA. Alajuela: *Lyon 381* (CR, MO); Cartago: *Crosby & Crosby 5848* (CR, MO); Heredia: *Crosby & Crosby 6061* (CR, FH, MO, NY, US); Limón: *Davidse et al. 28815* (MO, NY); Puntarenas: *Lyon 76* (CR, MO); San José: *Bowers 217* (CR, MO). PANAMA. Bocas del Toro: *Alfaro & Monro 5456* (BM, MEXU, MO, PMA); Chiriquí: *Folsom 6026* (F, MO, PMA, NY, US); Coclé: *Crosby 4406* (BM, DUKE, F, FH, H, MICH, MO, NY, PMA, US).

World range: Central America; Caribbean; Western and Northern South America, Brazil.

Thamniopsis undata is a robust, fairly common cloud forest species in Costa Rica and western Panama. The species has broad ecological amplitude but seems to be especially prevalent on rotting wood. *Thamniopsis undata* has monomorphic, lanceolate to ovate-lanceolate leaves that are erect to erect-spreading and strongly undulate whether wet or dry. Its gradually long-acuminate leaves have sharply serrate margins that are more or less bordered by several rows of long, narrow cells. The marginal teeth are usually long and narrow, while the long-hexagonal to long-rectangular cells are often porose. The setae of *T. undata* are extremely long, and its often pendent, cylindrical capsules have needle-like rostrate opercula. *Thamniopsis undata* has a perfectly hookeriaceous peristome, with especially well-developed dorsal trabeculae that strongly project laterally. The annulus of *T. undata* is strongly differentiated, but not nearly as well developed as that of *T. incurva*; it consists of 7–9 rows of oblate, reddish cells that are dehiscent at base and persistent on the operculum. The calyptrae are large, mitrate, irregularly lobed at base, and often sparsely hairy. There is a distinctive form of *T. undata* (nomenclaturally centered on *T. acicularis*) that is a somewhat smaller plant, with leaves that are constricted at the base of the acumina and that have weakly serrate margins with short teeth that are at times somewhat swollen.

Thamniopsis undata, *T. incurva*, *T. oedodontia*, and *T. steyermarkii* are large species that differ from most other Central American species of *Thamniopsis* in having monomorphic, variously serrate leaves. *Thamniopsis incurva*, the oddest in this group, has obovate, smooth leaves with obtuse to rounded acute apices, very broad (20–26 μm) upper leaf cells, bifid margins with short, swollen teeth, and costae that are smooth at back. *Thamniopsis oedodontia* differs from *T. undata* in having massive, greatly swollen, bifid teeth on the leaf margins, elimbate leaves, very long, linear-flexuose leaf cells, and considerably smaller sporophytes: setae 15–20 mm long; capsules 1.5–2.0 mm long; oper-

cula 0.75 mm long; annuli of 2–3 rows of cells; and calyptrae 1.5–2.0 mm long. *Thamniopsis steyermarkii* typically has smooth leaves, but the species is distressingly variable in this respect and most collections have at least some lightly undulate leaves. It differs from typical *T. undata* in having slenderly acuminate to subulate leaves that are abruptly constricted above to long, slender acumina or subulae. However, the *acicularis*-form of *T. undata* also has leaves constricted at the base of the acumina. *Thamniopsis steyermarkii* differs from all forms of *T. undata* in having costae that are smooth at back and linear, thick-walled upper leaf cells. *Thamniopsis glandulifera* is also similar to the *acicularis*-form of *T. undata* in having leaves that are constricted above to long acumina; it differs, though, in having high, spiculose-papillose leaf cells, smaller, smooth leaves (1.0–1.5 mm vs. 2.5–4.0 mm long), narrower upper leaf cells (3–4 μm vs. 3–14 μm wide), and non-swollen marginal teeth.

17. *Trachyxiphium* W. R. Buck, Brittonia 39: 219. 1987.

Plants small and slender, yellowish green, green, reddish yellow, or pale green, in loose or dense mats. Stems prostrate, irregularly branched; stems in cross section with 1–3 rows of somewhat small, firm-walled epidermal cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Dorsal and lateral leaves erect, erect-spreading, falcate-secund, or somewhat flattened, lightly contorted to twisted when dry, erect-spreading, flexuose when wet. Dorsal and lateral leaves lanceolate to ovate-lanceolate, broadly acute, or long, slenderly acuminate; margins coarsely serrate to dentate in upper 2/3, teeth at times swollen and bifid, serrate to subentire below, plane to erect; costae double, ending 2/3–3/4 the leaf length, weakly diverging throughout or parallel, serrate on back, projecting at the apices; cells homogenous or heterogeneous, smooth or prorate, long-rectangular to elongate-fusiform; basal cells near the insertions enlarged, oblong-rectangular; alar cells short-rectangular, otherwise undifferentiated. Ventral leaves erect, ovate-lanceolate, symmetric; margins serrate in upper 2/3, teeth elongate, rarely bifid, entire below; costae double, slender, ending 2/3 the leaf length, diverging throughout, unequal, smooth on back, not projecting at the apices; upper cells elongate-flexuose. Autoicous. Setae elongate, flexuose, smooth below, lightly papillose below capsules. Capsules inclined to pendent, short-cylindric, neck well developed; exothecial cells collenchymatous; stomata rudimentary, 3–5-celled, on neck; opercula conic-rostrate; annuli of 2–3 rows or 5–8 rows of quadrate cells separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome narrowly triangular with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface yellow above, red at base, densely and closely cross-striate below, coarsely papillose above, primary walls yellow, smooth, ventral (inner) surface hyaline to yellowish, deposition thin, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not perforate, cilia absent. Calyptrae mitrate, irregularly lobed at base, smooth or somewhat roughened, naked.

Buck (1987) established *Trachyxiphium* for nine species segregated from *Hookeriopsis*. The genus is restricted to the Western Hemisphere, and it consists of mostly slender plants that can be dark green to reddish yellow or pale green. *Trachyxiphium* species with a dark green to reddish yellow color have an aspect very similar to *Hypnum*, while pale green species superficially resemble *Leucomium*. The genus has an undifferentiated stem epidermis and elimbate, lanceolate to ovate-lanceolate leaves. *Trachyxiphium* exhibits strong leaf dimorphism, with the dorsal and lateral leaves often distinctly different from the ventral leaves. It is, however, the features of the dorsal and lateral leaves that characterize the genus. They are narrow, have margins coarsely serrate to dentate in the upper two-thirds, with the teeth often swollen and bifid, and strong double costae that are serrate at back and often project at the tips. The leaf cells are usually homogeneous, with the upper ones often strongly prorate. The sporophytes of *Trachyxiphium* are more or less typical for the Hookeriaceae, especially in peristome form, and they have the rudimentary 3–5-celled stomata that are characteristic of the family. One species, *T. hypnaceum*, has the curious, massive annulus (5–8 rows of cells, separating from capsule along a dehiscent zone at base and persistent on the operculum) that is a characteristic

feature of *Thamniopsis*. The present treatment recognizes five Central American species of *Trachyxiphium*, and it includes new synonymy as well as some synonymy that differs from that proposed by Buck (1987). There are presently eight species in *Trachyxiphium*, but more may be transferred to the genus from *Hookeriopsis* after the latter genus is fully revised.

Trachyxiphium can be confused with *Hookeriopsis*, *Brymela*, or *Thamniopsis*. *Hookeriopsis* and *Brymela* are similar to *Trachyxiphium* in having a sclerodermis rather than a hyalodermis on the outside layer of the stems. *Hookeriopsis* differs from *Trachyxiphium* in having leaves with short double costae (ending below midleaf). *Brymela* species differ from most species of *Trachyxiphium* in having weakly toothed leaf margins with teeth that are never swollen or bifid. In addition, the genus typically has smooth costae that only weakly project at the tips. *Trachyxiphium* and *Thamniopsis* are very similar, and it may be impossible to keep them separate. Both genera have thin-walled leaf cells, leaf margins with swollen, often bifid teeth, and strong costae that are often spined, crested, or have paired, bifid teeth. Most species of *Trachyxiphium* differ from *Thamniopsis* in having leaf cells that are homogeneous throughout and often prorate. Nevertheless, there are some *Trachyxiphium* species with heterogeneous, mostly smooth leaf cells very similar to those of *Thamniopsis*. The presence of a stem hyalodermis in *Thamniopsis* will usually separate that genus from *Trachyxiphium*. However, there are some *Thamniopsis* species in which the hyalodermis is poorly developed, and some *Trachyxiphium* species that seem to have a weakly developed hyalodermis. Further blurring the distinctiveness of the two genera is the fact that both exhibit strong leaf polymorphism, and a massive, persistent annulus is present in both genera.

The name *Trachyxiphium* combines the Greek *trachy-* (rough) and *xiph-* (sword-like) and refers to the coarsely toothed margins and strongly prorate leaf cells often found in the leaf apex.

1. Leaves acute to short-acuminate 2
1. Leaves long, slenderly acuminate to filiform-acuminate 3

2. Leaves shortly acute. . . . . 5. *T. variabile*
2. Leaves long-acute to broadly acuminate . . . . . 2. *T. hypnaceum*

3. Basal leaf cells thin-walled, somewhat enlarged and differentiated from the upper and median cells . . . . . 3. *T. repens*
3. Basal leaf cells firm- to thick-walled, neither enlarged nor differentiated from the upper and median cells 4

4. Median leaf cells between the costae less than 20 µm long . . . . . 4. *T. subfalcatum*
4. Median leaf cells between the costae to 50 µm long . . . . . 1. *T. guadalupense*

1. *Trachyxiphium guadalupense* (Brid.) W. R. Buck, Brittonia 39: 220. 1987. *Hypnum guadalupense* Brid., Muscol. Recent. Suppl. 2: 96. 1812. *Hookeria guadalupensis* (Brid.) Müll. Hal., Syn. Musc. Frond. 2: 212. 1851. *Hookeriopsis guadalupensis* (Brid.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 362. 1877. Protologue. [Guadeloupe] In Insulâ Guadalupâ havitat. E clar. *De Candolles* herbario.

Hookeria falcata Hook., Musci Exot. 1: 54. 1818. *Pterygophyllum falcatum* (Hook.) Brid., Bryol. Univ. 2: 353. 1827. *Hookeriopsis falcata* (Hook.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 363. 1877. Protologue. [Colombia] In convallibus Andium Granatensium inter Almaguer et Pasto, altitudine 1200–1500 hexapod. *Humboldt et Bonpland*.

Hookeriopsis bowersiana H. A. Crum, Bryologist 89: 25. 1986. Protologue. [Mexico] Sierra Juárez, above Tuxtepec, on upper surface of wet boulder in full shade, ca. 5400 ft., 27 Dec 1970, *A. J. Sharp 3915*. Type. Upper surface of boulder; wet, full shade. ca. 5400 ft. Sierra Juárez above Tuxtepec, Oaxaca; Mexico, 27 December 1970, *A. J. Sharp 3915* (MO, isotype), *syn. nov.*

Plants small and slender, 1–3 cm long, green or yellowish red, rarely pale green, in dense mats. Stems prostrate, irregularly branched, yellowish when young, red with age; stems in cross section with sclerodermis of 1–3 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia subfoliose, with thin-walled cells; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids

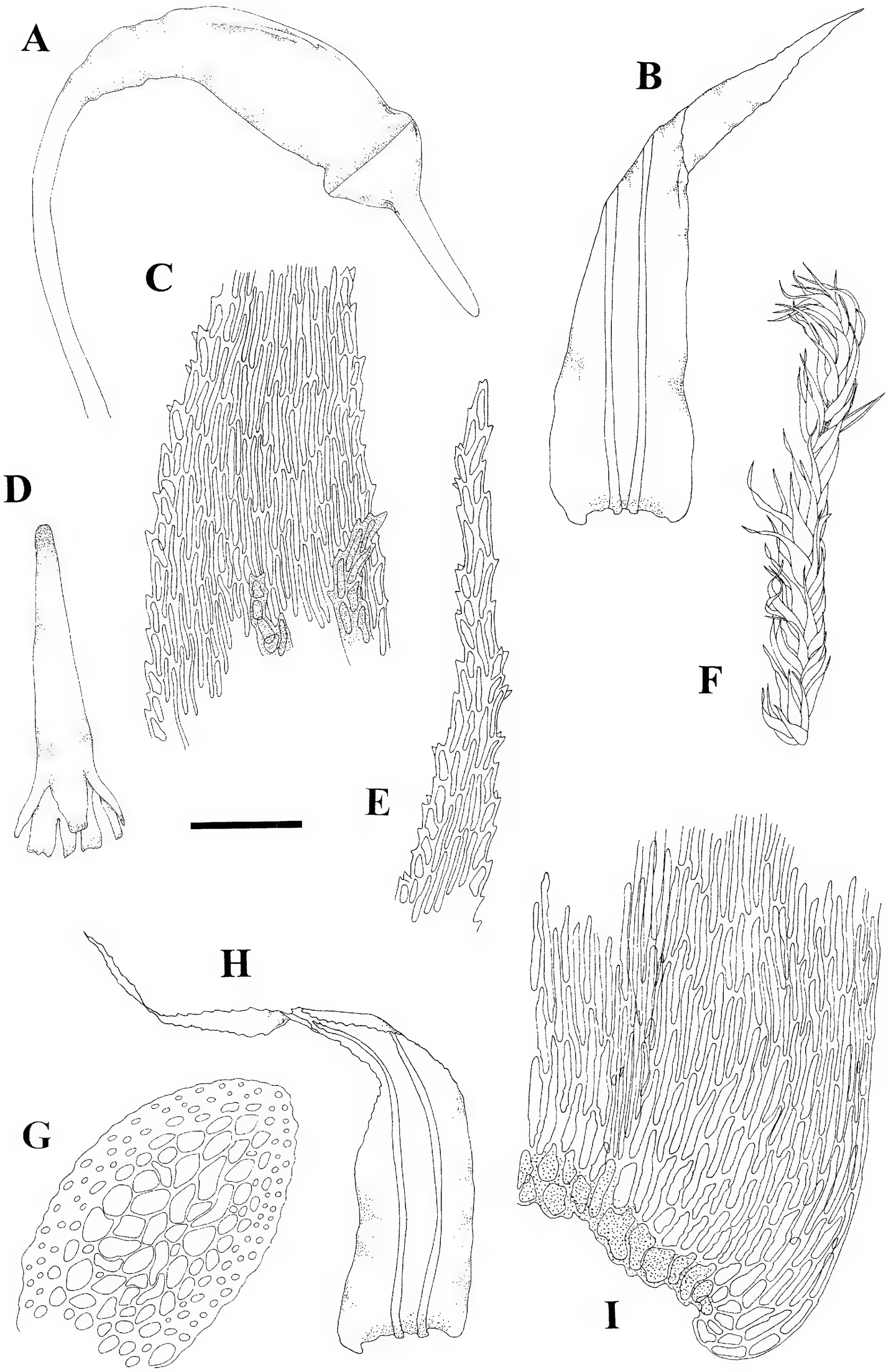
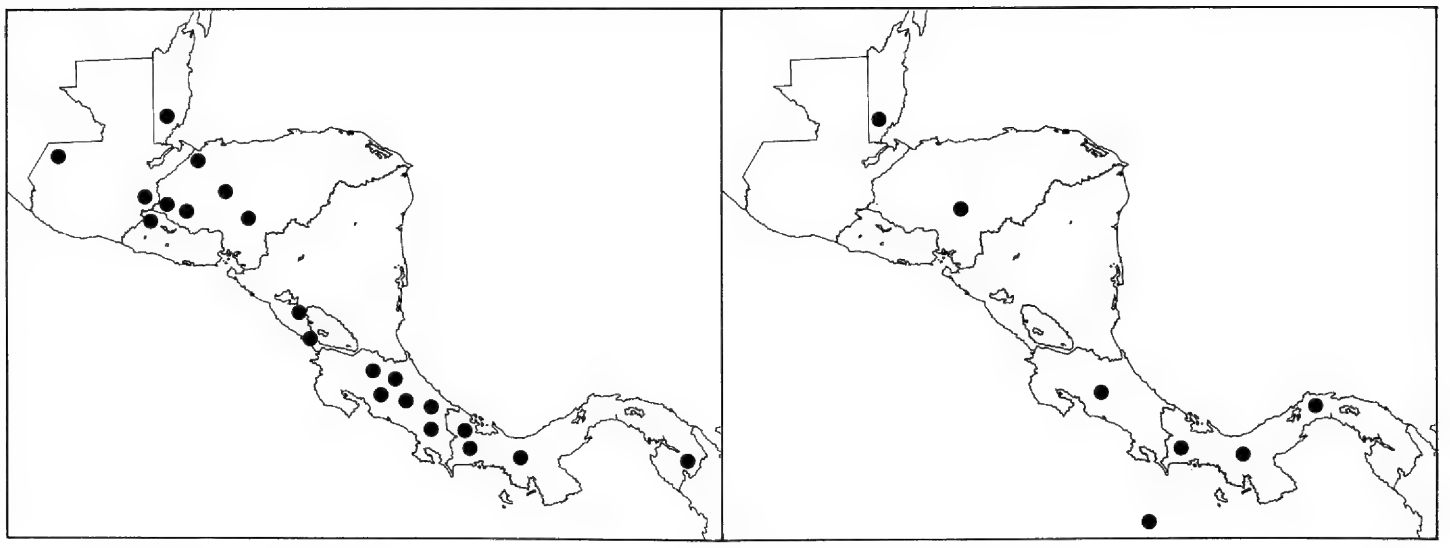


Figure 228. *Trachyxiphium guadalupense*. A. Seta, capsule, and operculum. B & H. Leaves. C. Upper leaf cells and margin including costal spine. D. Calyptra. E. Leaf apex. F. Habit. G. Stem in cross section. I. Basal and alar cells. Scale in mm: bar = 0.06 (C, E, I); bar = 0.08 (G); bar = 0.28 (B, H); bar = 0.6 (A, D); bar = 1.96 (F). A from *Crosby & Crosby 5823*; D from *Lyon 55*; all other figure parts from *Allen 14457*.



Trachyxiphium guadalupense *Trachyxiphium hypnaceum*

from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect at base, falcate-secund above when dry, erect-spreading, flexuose when wet. Dorsal and lateral leaves lanceolate to ovate-lanceolate, 1–2 mm long, gradually long-acuminate, often plicate; margins coarsely serrate to dentate in upper 2/3, teeth swollen, often bifid, serrate to subentire below, plane to erect; costae double, ending 2/3–3/4 the leaf length, weakly diverging throughout or parallel, serrate on back, projecting at the apices; cells smooth or prorate in upper 2/3, cells linear-flexuose throughout, firm-walled, eporose or porose, upper and median cells 20–50 × 2–3 µm, lower cells between the costae 40–60 × 2–3 µm; basal cells near the insertions enlarged, oblong-rectangular, often reddish brown across the base; alar cells short-rectangular, otherwise undifferentiated. Ventral leaves erect, lanceolate, symmetric; margins serrate in upper 2/3, teeth elongate, rarely bifid, entire below; costae double, slender, ending 2/3 the leaf length, diverging throughout, unequal, smooth on back, not projecting at the apices; upper cells elongate-flexuose. Autoicous. Setae elongate, 13–35 mm long, red, flexuose, smooth below, somewhat roughened to lightly scabrose below capsules. Capsules inclined to pendent, short-cylindric, 1.5–2.0 mm long, neck well developed; exothecial cells quadrate to oblate in 2–3 rows at mouth, those below oblong to rectangular, lateral walls evenly thickened, horizontal walls somewhat collenchymatous; stomata rudimentary, 3–5-celled, on neck; opercula conic-rostrate, 1.0 mm long; annuli of 2–3 rows of quadrate cells, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome narrowly triangular, with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface dark red, densely and closely cross-striate below, coarsely papillose above, primary walls yellow, smooth, ventral (inner) surface hyaline to yellowish, deposition thin, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not perforate, cilia absent. Spores rounded, 10–14 µm, smooth to faintly roughened. Calyptrae mitrate, 2.0–2.5 mm, yellowish white, red at times near apex, irregularly lobed at base, smooth or somewhat roughened, naked.

Illustrations. Bartram (1949, Fig. 135 J–L, as *Hookeriopsis subfalcata*); Welch (1969, Figs. 106–111); Welch (1974, Figs. 248 & 252, as *Hookeriopsis subfalcata*); Crum (1986, Figs. 18–21); Florschütz-de Waard (1986, Fig. 121); Sharp *et al.* (1994, Fig. 597 a–d); Duarte Bello (1997, Pls. 244 & 245); Buck (1998, Pl. 27 1–8); Gradstein *et al.* (2001, Fig. 170 F–K); Buck (2003, Fig. 102); Vaz and Costa (2006a, Figs. 113–121). Figure 228.

Habitat. On decorticated, rotting logs, branches, twigs, tree roots, filmy fern leaves, and rocks or boulders on forest floor and along or in streams; 580–2600 m.

Distribution in Central America. BELIZE. Toledo: *Whittemore 6507* (BRH, MO). GUATEMALA. Chiquimula: *Steyermark 31018* (F, FH, NY); Huehuetenango: *Steyermark 48790* (F, FH, NY). EL SALVADOR. Santa Ana: *Watson ES-0003* (MO). HONDURAS. Comayagua: *Allen 13875*

(MO); Cortés: *Allen 14305* (MO, TEFH); Francisco Morazán: *Standley et al. 5076* (F, FH); Lempira: *Allen 11522* (MO, TEFH); Ocotepeque: *Allen 14457* (MO, TEFH). NICARAGUA. Granada: *Croat 39144* (MO); Rivas: *Hahn 508* (MO). COSTA RICA. Alajuela: *Lyon 55* (CR, MO); Cartago: *Gómez 19372* (CR, MO); Heredia: *Crosby & Crosby 6041* (MO); Limón: *Croat 43342* (CR, MO); Puntarenas: *Lyon 263* (CR, MO); San Jose: *Crosby & Crosby 5871* (MO). PANAMA. Bocas del Toro: *Hammel 6114* (MO, PMA); Chiriquí: *Crosby 4050* (MO, NY, PMA); Darién: *Mori & Gentry 4486* (MO); Veraguas: *Mori 6736* (MO).

World range: Mexico; Central America; Caribbean; Western and Northern South America.

Trachyxiphium guadalupense is a slender, usually green or yellowish red species that has wide ecological amplitude. It has slenderly acuminate, lanceolate to ovate-lanceolate leaves that are stiffly erect at base but falcate-secund above, and this gives them an aspect very similar to some species of *Hypnum*. The leaves have long double costae that are usually serrate at back and toothed at the tips; margins with enlarged, often bifid serrations or dentations; firm-walled, linear-flexuose cells; undifferentiated alar cells; and short-rectangular, usually dark reddish cells across the leaf insertions. Most plants of *T. guadalupense* have prorate upper leaf cells; however, the degree of papillosity on individual leaves varies from entirely smooth to moderately or strongly prorate. The sporophytes of *T. guadalupense* are typical for the Hookeriaceae. Its setae, however, are unusually long for an otherwise small species.

In Central America *Trachyxiphium guadalupense* can be difficult to distinguish from *T. subfalcatum*, *T. repens*, and *T. hypnaceum*. All three species usually have pale greenish plants that differ from *T. guadalupense* in their laxly erect rather than stiffly erect leaves. *Trachyxiphium subfalcatum* further differs from *T. guadalupense* in having shorter leaf cells (15–30 µm vs. 20–50 µm) that are consistently strongly prorate. The leaves of *T. repens* and *T. guadalupense* are identical in outline, but their areolation is quite different. In *T. repens* the thin-walled, somewhat enlarged basal cells are differentiated from the upper and median cells, while in *T. guadalupense* the firm- to thick-walled basal leaf cells are not distinctly differentiated from the upper and median cells. *Trachyxiphium hypnaceum* also differs from *T. guadalupense* in having long-acute rather than slenderly acuminate leaves. The leaf apex difference between *T. hypnaceum* and *T. guadalupense* is best seen by examining their stem and branch tips. In *T. hypnaceum* these leaves are erect to somewhat curved. In contrast, these leaves in *T. guadalupense* are strongly and distinctly falcate-secund. Although *Thamniopsis glandulifera* has sometimes been confused with *T. guadalupense*, it differs in having leaves that are abruptly constricted above to long, slender acumina, papillose-spiculose leaf cells, and a weak stem hyalodermis.

2. *Trachyxiphium hypnaceum* (Müll. Hal.) W. R. Buck, Brittonia 39: 220. 1987. *Hookeria hypnacea* Müll. Hal., Bot. Zeitung (Berlin) 14: 421. 1856. *Hookeriopsis hypnacea* (Müll. Hal.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 364. Protologue. Brasilia, Sa Catharina, in truncis putridis prope Rio du Velba, Julio: *Pabst* inter *Hypnum rutilans* et *brachyneuron* misit. Type. Brazil, Santa Catharina, *Pabst*, 1851 (BM, isotype).

Hookeria gracilis Mitt., J. Linn. Soc., Bot. 12: 360. 1869. *Hookeriopsis gracilis* (Müll. Hal.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 362. 1877. Protologue. [Ecuador] Andes Quitenses, *Jameson*; in sylva Canelos, *Spruce*. Type (see Buck 1987). Mont. de Canelos, *Spruce* (NY, lectotype), *syn. nov.*

Hookeriopsis heteroica Cardot, Rev. Bryol. 37: 51. 1910. *Trachyxiphium heteroicum* (Cardot) W. R. Buck, Brittonia 39: 220. 1987. Protologue. [Mexico] État de Vera-cruz: près de Jalapa, sur bois pourri, 1908 [*Pringle*] (*n° 15145*). Types. Plantae Mexicanae. Vera Cruz, on old wood in a brook, Jalapa, 28 June, 1908, *C. G. Pringle 15145* (FH, MO, US, isotypes), *syn. nov.*

Plants small and slender, 1–3 cm long, pale green to green, in loose or dense mats. Stems prostrate, irregularly branched, whitish to yellowish when young, red with age; stems in cross section with 1–3 rows of somewhat enlarged, firm-walled epidermal cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect to erect-spreading, somewhat contorted to twisted when dry, erect-

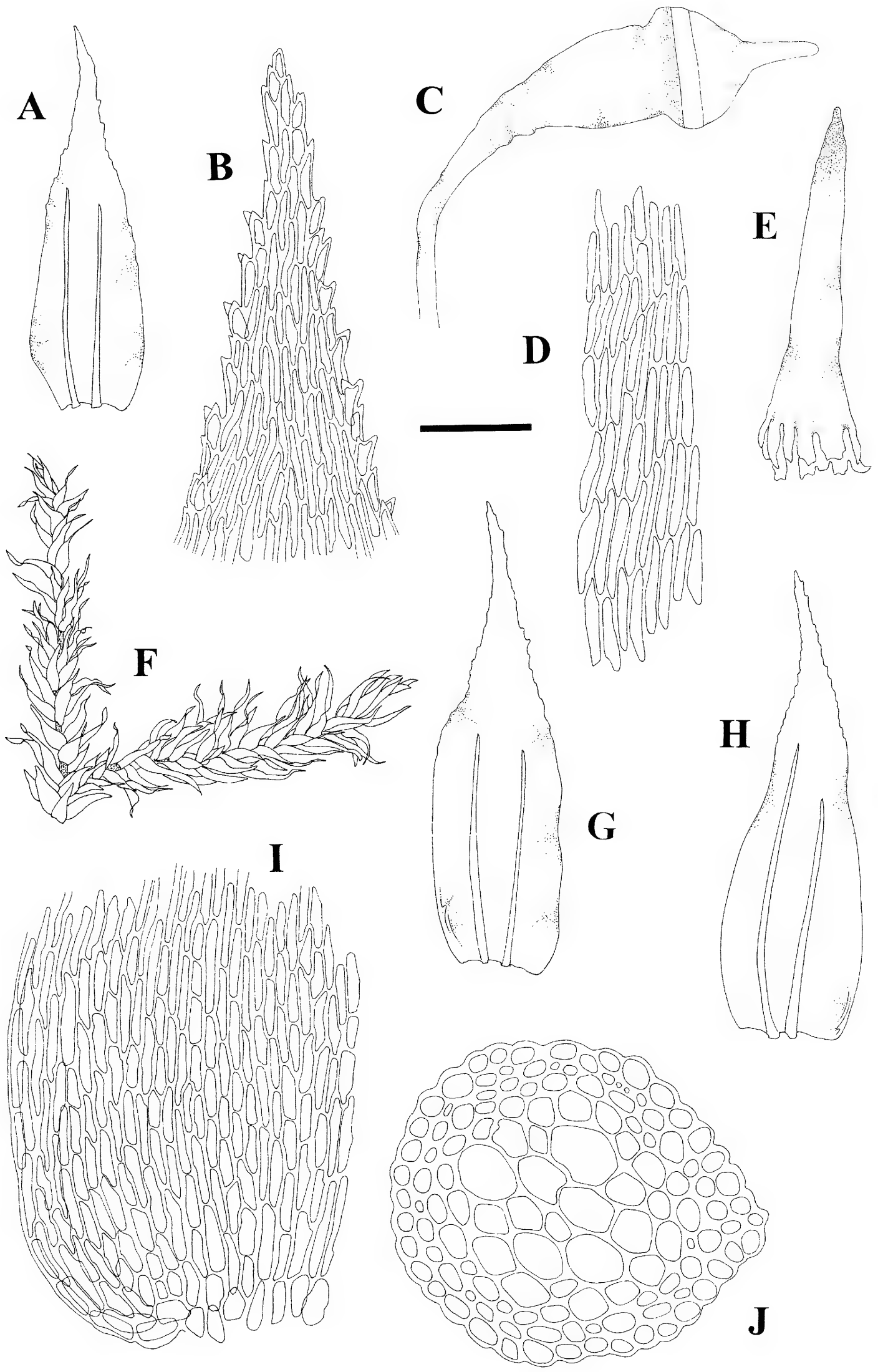


Figure 229. *Trachyxiphium hypnaceum*. A, G & H. Leaves. B. Leaf apex. C. Seta, capsule, annulus, and operculum. D. Median leaf cells. E. Calyptra. F. Habit. I. Basal and alar cells. J. Stem in cross section. Scale in mm: bar = 0.06 (B, D, I, J); bar = 0.26 (C); bar = 0.36 (E); bar = 0.7 (A, G, H); bar = 1.56 (F). A, D, G–I from *Pringle 15145* (type *T. heteroica*); B from *Gordon 3674*; C, E from *Allen 15474*; all other figure parts from *Whittemore 6370*.

spreading, flexuose when wet. Dorsal and lateral leaves lanceolate to ovate-lanceolate, 1.0–1.4 mm long, gradually long-acute to broadly acuminate; margins coarsely serrate to dentate in upper 2/3, teeth swollen, often bifid, serrate to subentire below, plane to erect; costae double, ending 2/3–3/4 the leaf length, weakly diverging throughout or parallel, serrate on back, projecting at the apices; cells smooth, at times weakly prorate near apex, long-rectangular to elongate-fusiform, thin-walled, eporose, 25–50 × 4–6 µm, lower cells between the costae 40–50 × 4–6 µm; basal cells near the insertions enlarged, oblong-rectangular; alar cells short-rectangular, otherwise undifferentiated. Ventral leaves erect, lanceolate, symmetric; margins serrate in upper 2/3, teeth elongate, rarely bifid, entire below; costae double, slender, ending 2/3 the leaf length, diverging throughout, unequal, smooth on back, not projecting at the apex; upper cells elongate-flexuose. Autoicous. Setae elongate, 8–15 mm long, red, flexuose, smooth throughout or at times roughened to scabrose below capsules. Capsules inclined to pendent, short-cylindric, 1.0 mm long, neck well developed; exothecial cells quadrate to oblate in 2–3 rows at mouth, those below oblong to rectangular, thick-walled, collenchymatous; stomata rudimentary, 3–4-celled, on neck; opercula conic-rostrate, 0.5 mm long; annuli of 5–8 rows of cells, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome narrowly triangular with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface yellow above, red at base, densely and closely cross-striate below, coarsely papillose above, primary walls yellow, smooth, ventral (inner) surface hyaline to yellowish, deposition thin, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not perforate, cilia absent. Spores rounded, 8–10 µm, smooth to faintly roughened. Calyptrae mitrate, 1.0 mm long, yellowish white, at times red near apices, irregularly lobed at base, smooth or somewhat roughened, naked.

Illustrations. Welch (1969, Figs. 144–149); Crum and Anderson (1981, Fig. 396); Crum (1986, Figs. 14–17); Sharp *et al.* (1994, Fig. 597 e–h). Figure 229.

Habitat. On rotting logs or rocks along and in streams and on rotting wood in forests; 600–2000 m.

Distribution in Central America. BELIZE. Toledo: *Whittemore 6370* (BR, MO, NY). HONDURAS. Francisco Morazán: *Allen 12367* (MO). COSTA RICA. Puntarenas: Cocos Island, *Weber B-14082* (US); San José: *Holz 356* (NY). PANAMA. Chiriquí: *Salazar et al. 5404* (MO, PMA); Panamá: *Welch 19976* (NY); Veraguas: *Crosby 10177* (MO).

World range: Southeastern U.S.A.; Mexico; Central America; Western South America, Brazil.

Trachyxiphium hypnaceum is a slender species, with usually pale green plants and laxly erect to erect-spreading leaves that are somewhat crispate to flexuose when dry. Its lanceolate to ovate-lanceolate leaves are long-acute to broadly acuminate, and the areolation, although homogeneous, consists of lax and fairly broad cells. The lateral and dorsal leaves in *T. hypnaceum* have sharply serrate upper margins with swollen, often bifid teeth, and the costae are serrate on the dorsal surface and consistently project at the tips. *Trachyxiphium hypnaceum* has small, slender sporophytes, and, unlike for most members of the genus, the opercula are massive, consisting of 5–8 rows of pale brownish cells that are persistent on the operculum. This type of annulus, although characteristic of *Thamniopsis*, is not consistently present in that genus. Central American plants of *T. hypnaceum* have setae smooth throughout or faintly roughened just below the capsule, but some South American collections (*i.e.*, the Ecuadorian type of *Hookeria gracilis* Mitt.) have setae papillose to scabrous below the capsule.

Trachyxiphium variabile and *T. repens* can be confused with *T. hypnaceum* because they all have a pale green color and lax basal cells. *Trachyxiphium variabile* and *T. hypnaceum* are especially close, and they differ only in leaf shape: *T. variabile* has shortly acute leaves; *T. hypnaceum* has long-acute to shortly acuminate leaves. *Trachyxiphium repens* differs from *T. hypnaceum* in having long, slenderly acuminate to filiform-acuminate leaves, with a heterogeneous leaf areolation in which the enlarged basal cells contrast strongly with the narrow upper and median cells. *Trachyxiphium guadalupense* is the most common Central American species in the genus, and it differs from *T. hypnaceum* in its green to yellowish red color and firm, slenderly acuminate to filiform-acuminate leaves that have longer, firm- to thick-walled, usually prorate cells. It also has larger sporophytes than *T. hypnaceum*: setae 13–35 mm vs. 8–12 mm long; capsules 1.5–2.0 mm vs. 1.0 mm long.

In the field *Trachyxiphium hypnaceum* has an aspect nearly identical to *Leucomium* or *Rhynchostegiopsis*. These genera differ from *T. hypnaceum* in having ecostate leaves and cucullate calyptrae. *Leucomium* also has entire leaf margins.

3. *Trachyxiphium repens* (Hook. & Grev.) B. H. Allen, *comb. nov.* Basionym: *Hookeria repens* Hook. & Grev., Edinburgh J. Sci. 2: 231. 1825. Protologue. St. Vincents, *Rev. L. Guilding*. Type. St. Vincent, *Guilding* (NY, isotype).

Plants small and slender, 1–3 cm long, pale green, green, rarely yellowish red, in dense mats. Stems prostrate, irregularly branched, yellowish when young, red with age; stems in cross section with sclerodermis of 1–3 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia subfoliose, thin-walled; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect at base, falcate-secund above when dry, erect-spreading, flexuose when wet. Dorsal and lateral leaves lanceolate to ovate-lanceolate, 1.0–1.5 mm long, gradually long-acuminate, at times somewhat undulate; margins coarsely serrate to dentate in upper 2/3, teeth swollen, often bifid, serrate to subentire below, plane to erect; costae double, ending 2/3–3/4 the leaf length, weakly diverging throughout or parallel, serrate on back, projecting at the apices; cells smooth or prorate in upper 2/3, upper and median cells linear-flexuose, firm-walled, eporose or porose, 50–60 × 4–6 µm, lower cells between the costae 60–80 × 4–6 µm; basal cells enlarged, oblong-rectangular; alar cells short-rectangular, otherwise undifferentiated. Ventral leaves erect, lanceolate, symmetric; margins serrate in upper 2/3, teeth elongate, rarely bifid, entire below; costae double, slender, ending 2/3 the leaf length, diverging throughout, unequal, smooth on back, not projecting at the apices; upper cells elongate-flexuose. Autoicous. Setae elongate, 8–14 mm long, red, flexuose, smooth below, somewhat roughened below capsules. Capsules erect, horizontal or inclined, short-cylindric, 1.0–1.5 mm long, neck well developed; exothecial cells quadrate to oblate in 2–3 rows at mouth, those below oblong to rectangular, lateral walls evenly thickened, horizontal walls somewhat collenchymatous; stomata rudimentary, 3–4-celled, on neck; opercula conic-rostrate, 0.5–0.7 mm long; annuli of 2–3 rows of quadrate cells, separating from capsule along dehiscent zone at base and persistent on the operculum; peristome diplolepideous, exostome narrowly triangular, with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface dark red, densely and closely cross-striate below, coarsely papillose above, primary walls yellow, smooth, ventral (inner) surface hyaline to yellowish, deposition thin, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not perforate, cilia absent. Spores rounded, 8–16 µm, smooth to faintly roughened. Calyptrae mitrate, 1.0–1.5 mm long, yellowish white, red at times near apex, irregularly lobed at base, smooth or somewhat roughened, naked.

Illustration. Figure 230.

Habitat. On rotting logs or branches, and humus; 300–2100 m.

Distribution in Central America. COSTA RICA. Alajuela: *Crosby 10022* (CR, MO, NY, US); Heredia: *Skutch 3238* (FH, MO, NY, US); Limón: *Svihla 3034* (FH); Puntarenas: *Lyon 42* (CR, FH, MO, NY); San José: *Crosby & Crosby 5969* (CR, F, MO). PANAMA. Bocas del Toro: *Allen 5611* (MO, PMA); Chiriquí: *Folsom et al. 5524* (MO); Coclé: *Folsom 6506* (MO); Darién: *Folsom 6399* (MO, PMA); Veraguas: *Nee & Mori 14337* (MO).

World range: Central America; Caribbean.

Trachyxiphium repens is a slender, silky species with usually pale green plants and slenderly acuminate, falcate-secund, lanceolate to ovate-lanceolate leaves. The most distinctive feature of the species is its heterogeneous leaf areolation: upper cells linear-flexuose; and basal cells enlarged, oblong-rectangular. The leaf cells are usually smooth, lax, and fairly wide throughout. The leaves are strongly dimorphic: dorsal and lateral leaves slender, with long costae that are serrate at back and toothed at the tips, and margins with enlarged, often bifid serrations or dentations; and ventral leaves broad, with weak costae that are smooth at back and do not project at the tips, and weakly serrate margins. The

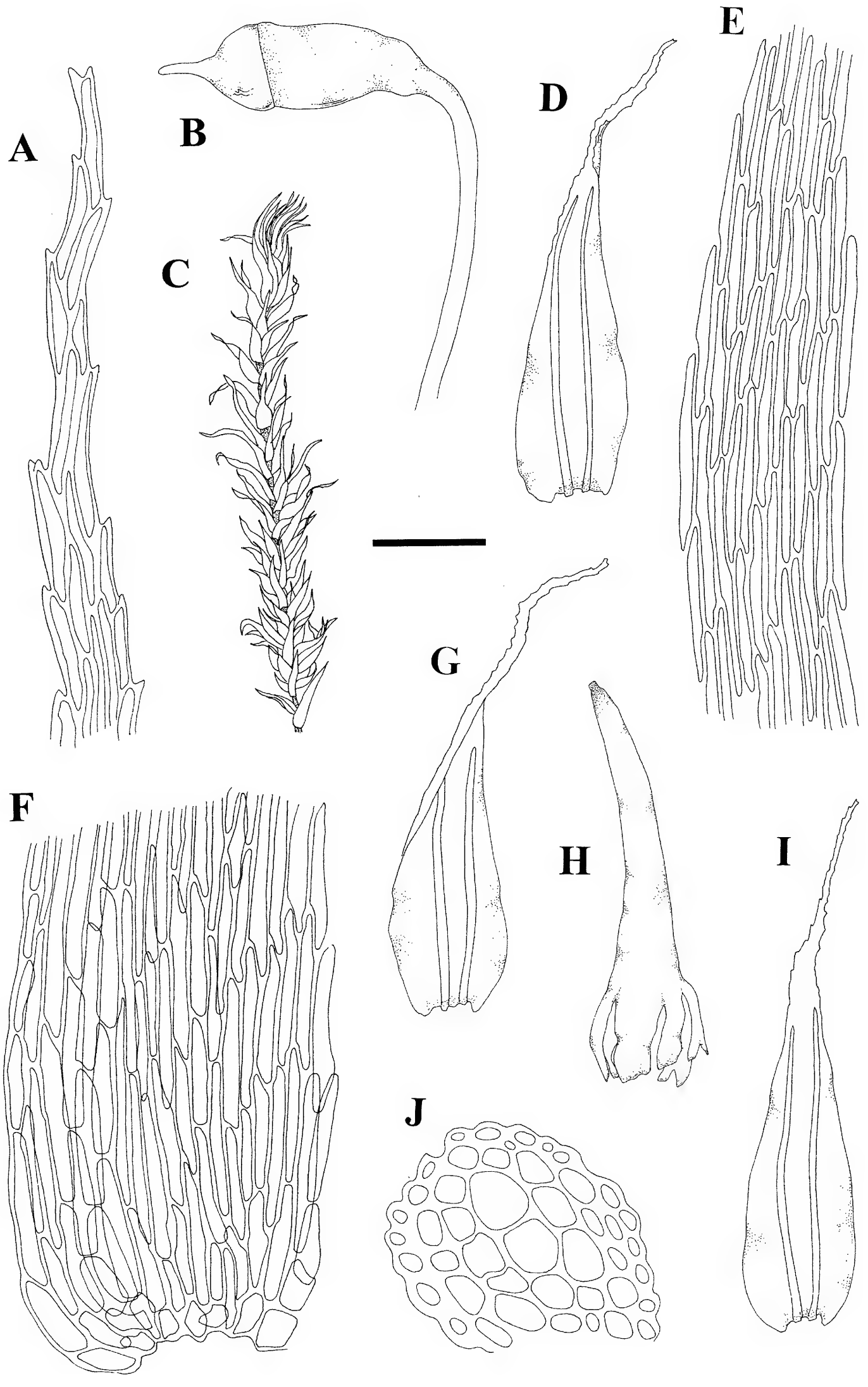
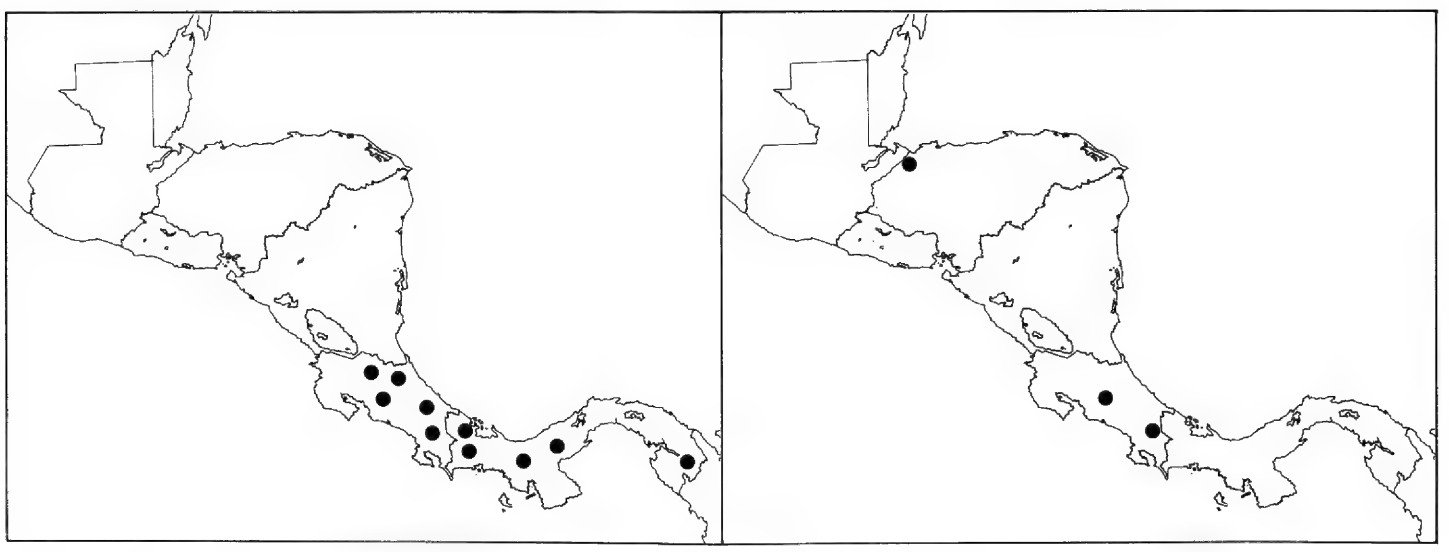


Figure 230. *Trachyxiphium repens*. A. Leaf apex. B. Seta, capsule, and operculum. C. Habit. D, G & I. Leaves. E. Median leaf cells between the costae. F. Basal and alar cells. H. Calyptra. J. Stem in cross section. Scale in mm: bar = 0.05 (A, E, F); bar = 0.06 (J); bar = 0.28 (D, G, I); bar = 0.36 (H); bar = 0.5 (B); bar = 1.56 (C). All figure parts from *Crosby 10022*.



Trachyxiphium repens *Trachyxiphium subfalcatum*

ventral leaves also have more homogeneous leaf cells, with mostly linear-flexuose cells throughout. The sporophytes of *T. repens* are small and slender.

In Central America *Trachyxiphium repens* is often confused *T. guadalupense*, because the two species sometimes occur in mixed collections and have identically shaped leaves. Indeed, *T. repens* has long been considered a synonym of *T. guadalupense*. *Trachyxiphium guadalupense* differs from *T. repens* in having shiny, green or yellowish red plants with firm-walled, often prorate, linear-flexuose cells throughout the leaves. In addition its sporophytes are considerably larger (setae 13–35 mm vs. 8–14 mm long; capsules 1.5–2.0 mm vs. 1.0–1.5 mm long) than those of *T. repens.*

Trachyxiphium variabile and *T. hypnaceum* have also been confused with *T. repens* because they all have pale green plants, lax basal cells, and small, slender sporophytes. The three species differ in leaf apex shape: *T. variabile* with acute leaves; *T. hypnaceum* with long-acute to shortly acuminate leaves; *T. repens* with very long, slenderly acuminate to filiform-acuminate leaves. The gametophytes of *T. hypnaceum* also differ from those of *T. repens* in having homogeneous leaf cells, while its sporophytes differ in having massive annuli of 5–8 rows of pale brownish cells that are persistent on the operculum.

4. *Trachyxiphium subfalcatum* (Hampe) W. R. Buck, Brittonia 39: 220. 1987. *Hookeria subfalcata* Hampe, Ann. Sci. Nat., Bot. sér. 5, 5: 305. 1866. *Hookeriopsis subfalcata* (Hampe) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 362. 1877. Protologue. [Colombia] Hab. Bogota, Tequendama, Pacho et Canoas. 2000–2500 m, in sylv., martio et angusto copiose leg. *A. Lindig*.

Hookeria adunca Mitt., J. Linn. Soc., Bot. 12: 362. 1869. *Trachyxiphium aduncum* (Mitt.) W. R. Buck, Brittonia 39: 220. 1987. Protologue. Andes Peruvianae, Tarapoto ad caput fl. Cumbasa, in trunco carioso, *Spruce, n. 650*. Type. Andes Peruvianae, ad caput. fl. Canbusa, in trunco emortuo humido, *Spruce 650* (NY, holotype), *syn. nov.*

Hookeria asprella Hampe, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn ser. 3, 9–10: 266. 1878. Protologue. [Brazil] Sub *nr. 9081*, *9082*, *9085*. [In vicinia urbis Rio de Janeiro lecti *A. Glaziou*.] Type. *Glaziou 9085* (NY, lectotype [Buck 1987]), *syn. nov.*

Hookeria viridissima Mitt., J. Linn. Soc., Bot. 12: 362. 1869. *Hookeriopsis viridissima* (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 363. 1877. Protologue. [Colombia] Nova Granata; fl. Magdalena, in sylvis humidis ad terram super ramulos emortuos repens (500 ped.), *Weir 381*. Type. Rio Magdalena, rotten sticks, moist forest, *Weir 381* (NY, holotype).

Plants small and slender, 1–3 cm long, green to pale green, in dense mats. Stems prostrate, irregularly branched, yellowish when young, red with age; stems in cross section with sclerodermis of 1–3 rows of small, thick-walled cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia subfoliose, with thin-walled cells; axillary hairs 2-celled, basal

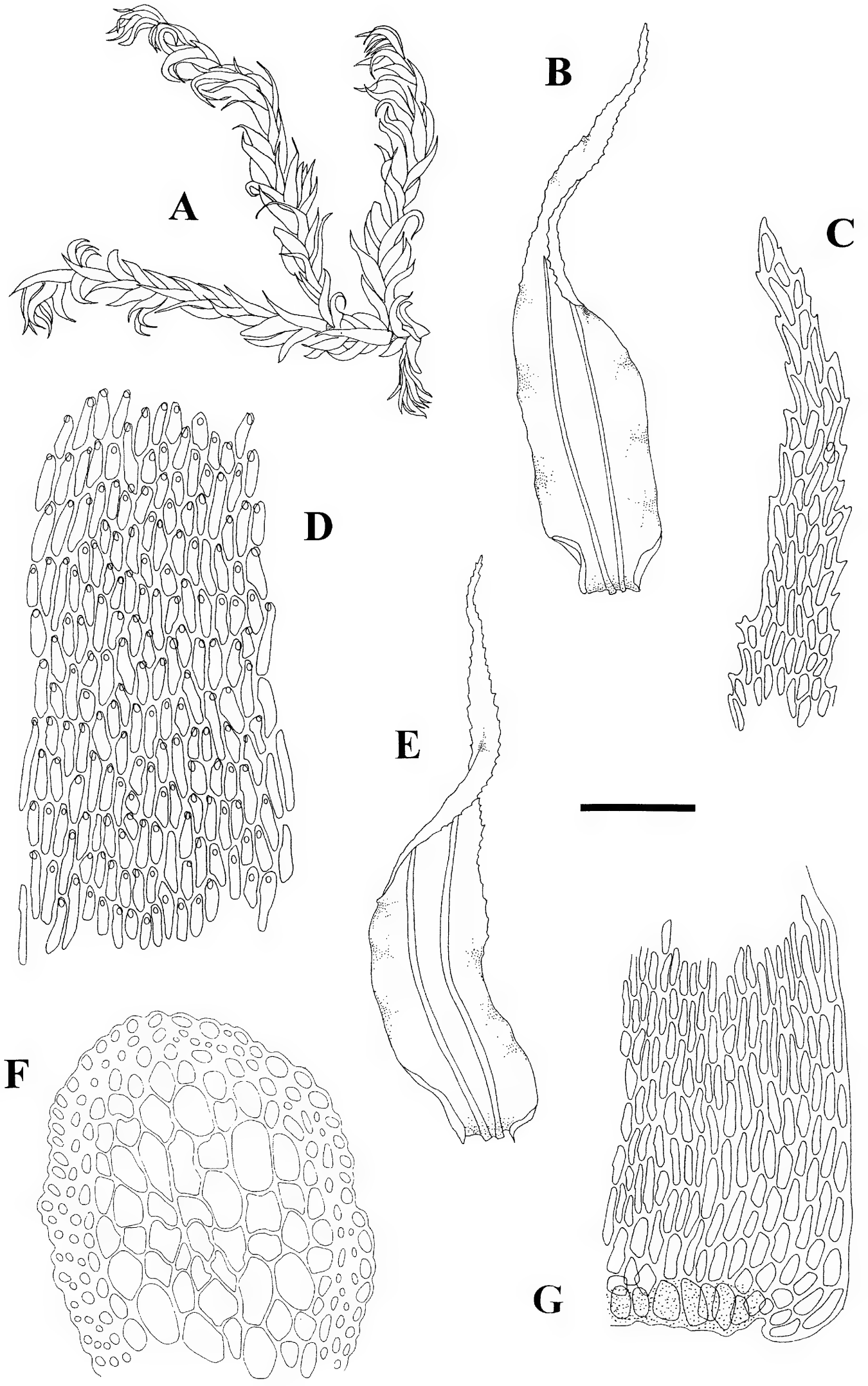


Figure 231. *Trachyxiphium subfalcatum*. A. Habit. B & E. Leaves. C. Leaf apex. D. Upper leaf cells. F. Stem in cross section. G. Basal and alar cells. Scale in mm: bar = 0.05 (C, D, G); bar = 0.08 (F); bar = 0.28 (B, E); bar = 1.56 (A). B, E from *Allen 14396*; F from *Lindig 2150*; all other figure parts from *Holz CR00-0765*.

cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect at base, falcate-secund above when dry, erect-spreading, flexuose when wet. Dorsal and lateral leaves lanceolate to ovate-lanceolate, 1.0–1.5 mm long, gradually long-acuminate; margins coarsely serrate to dentate in upper 2/3, teeth swollen, often bifid, serrate to subentire below, plane to erect; costae double, ending 2/3–3/4 the leaf length, weakly diverging throughout or parallel, serrate on back, projecting at the apices; cells densely prorate, upper and median cells long-rectangular, 15–30 µm long, firm-walled, eporose or porose, lower cells between the costae 14–40 × 2–6 µm; basal cells near the insertions enlarged, oblong-rectangular, often reddish brown across the base; alar cells short-rectangular, otherwise undifferentiated. Ventral leaves erect, lanceolate, symmetric; margins serrate in upper 2/3, teeth elongate, rarely bifid, entire below; costae double, slender, ending 2/3 the leaf length, diverging throughout, unequal, smooth on back, not projecting at the apices; upper cells elongate-flexuose. Autoicous. Setae elongate, 12–22 mm long, red, flexuose, smooth below, somewhat roughened below capsules. Capsules inclined to pendent, short-cylindric, 1.5–2.0 mm long, neck well developed; exothecial cells quadrate to oblate in 2–3 rows at mouth, those below oblong to rectangular, lateral walls evenly thickened, horizontal walls collenchymatous; stomata rudimentary, 3–4-celled, on neck; operculum and annulus not seen; peristome diplolepideous, exostome narrowly triangular with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface dark red, densely and closely cross-striate below, coarsely papillose above, primary walls yellow, smooth, ventral (inner) surface hyaline to yellowish, deposition thin, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not perforate, cilia absent. Spores rounded, 8–10 µm, smooth to faintly roughened. Calyptrae mitrate, 2.0 mm long, yellowish white below, red above, irregularly lobed at base, smooth or somewhat roughened, naked.

Illustrations. Vaz and Costa (2006a, Figs. 105–112, as *T. aduncum*). Figure 231.

Habitat. On tree trunks, soil, and rocks in or near streams; 1510–2200 m.

Distribution in Central America. HONDURAS. Cortés: *Allen 14351* (MO). COSTA RICA. Puntarenas: *Lyon 495* (MO); San José: *Standley 41971* (FH, NY, US).

World range: Central America; Western South America, Brazil.

Trachyxiphium subfalcatum is a slender species with slenderly acuminate, lanceolate to ovate-lanceolate leaves that are erect at base and falcate-secund above. The leaves have long double costae that are usually serrate at back and toothed at the tips; margins with enlarged, often bifid serrations or dentations; and long-rectangular leaf cells that are firm-walled, remarkably short for the genus, and densely prorate nearly throughout. The leaf cells are sometimes spiculose-papillose in the same degree as the cells of *Thamniopsis glandulifera*. The sporophytes of *T. subfalcatum* are typical for the Hookeriaceae.

In Central America *Trachyxiphium subfalcatum* can be especially difficult to distinguish from *T. guadalupense* because their plants are identical in overall aspect and leaf shape. *Trachyxiphium guadalupense* differs from *T. subfalcatum* in having longer, broader leaf cells (long-rectangular, 15–30 µm vs. linear-flexuose, 20–50 µm long). Although there is considerable overlap in their cell size ranges, most cells in *T. subfalcatum* are in the 15–20 µm range, while *T. guadalupense* usually has leaf cells in the 40–50 µm range. Furthermore, the leaf cells of *T. guadalupense* are less strongly prorate (sometimes smooth) than those of *T. subfalcatum*, and never spiculose-papillose.

Trachyxiphium repens can also be confused with *T. subfalcatum* because they both have long, slenderly acuminate to filiform-acuminate leaves. *Trachyxiphium repens* differs from *T. subfalcatum* in having pale greenish plants with laxly erect rather than stiffly erect leaves and smooth or prorate upper cells that are never spiculose-papillose. In addition, *T. repens* differs from *T. subfalcatum* in having thin-walled, somewhat enlarged, rectangular basal cells. *Thamniopsis glandulifera* and *Trachyxiphium subfalcatum* both have densely prorate (usually spiculose-papillose) leaf cells, and this may cause some confusion between them. *Thamniopsis glandulifera* differs from *Trachyxiphium subfalcatum* in having leaves that are abruptly constricted above to long, slender acumina, and a stem hyalodermis.

5. *Trachyxiphium variabile* (Hornsch. *ex* Mitt.) W. R. Buck, Brittonia 39: 221. 1987. *Hookeria variabilis* Mitt., J. Linn. Soc., Bot. 12: 359. 1869. *Hookeriopsis variabilis* (Hornsch. *ex* Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 362. 1877. Protologue. [Colombia] Andes Bogotenses, *Weir, n. 149*; Brasilia, Sierra dos Orgaos, in truncis emortuis sylvarum antiquissimarum, *Beyrich*; Rio de Janeiro, *Gardner*; ad viam inter San Paulo et Jundiahy prope Olha da Agua (1800 ped.) *Weir*. Type (see Buck 1987). Brazil, Rio de Janeiro, *Gardner* (NY, lectotype).

Hookeria planiuscula Hampe, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn ser. 3, 6: 161. 1875. *Hookeriopsis planiuscula* (Hampe) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 364. 1877. Protologue. [Brazil] Sub *Nr. 7152*, *7164* parce intermixta lecta. [*A. Glaziou* in vicinia urbis Rio de Janeiro.] Type (see Buck 1987). Brazil. Rio de Janeiro, *Glaziou 7152* (NY, isolectotype).

Hookeria tenera Hampe, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn ser. 3, 6: 161. 1875. *Hookeriopsis tenera* (Hampe) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 364. 1877. Protologue. [Brazil] Inter *Hookeriam hypnaceam* parcissime lecta. [*A. Glaziou* in vicinia urbis Rio de Janeiro.] Type. Brazil. Rio de Janeiro, *Glaziou 6354 p.p.* (BM, holotype).

Hookeria subaurescens Geh. & Hampe *in* Geh., Flora 64: 411. 1881. *Hookeriopsis subaurescens* (Geh. & Hampe) Broth., Nat. Pflanzenfam. I(3): 939. 1907. Protologue. [Brazil] Prope Apiaphy, Majo 1879: *Puiggari 641*[b]. [Rio de Janeiro and São Paulo]. Type. Brazil, Sao Paulo, Apiahy, *Puiggari 641*[b], 1879 (BM, isotype), *syn. nov.*

Hookeria tenuis Mitt., J. Linn. Soc., Bot. 12: 355. 1869. *Hookeriopsis tenuis* (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 360. 1877. *Trachyxiphium tenue* (Mitt.) W. R. Buck, Brittonia 39: 220. 1987. Protologue. Andes Peruvianae, in monte Campana (3000 ped.), *Spruce, n. 637*; Tarapoto (2000 ped.), *Spruce, n. 638*; in monte Guayrapurina (2500 ped.), *Spruce n. 639*; ad fl. Huallaga (1300 ped.), *Spruce, n. 640*; ad rivulum Shillicaio (2000 ped.), *Spruce, n. 641*. Type (see Buck 1987). Shillicaia, *Spruce 641* (NY, lectotype), *syn. nov.*

Hookeria leucomioides Broth., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 26 Afd. 3(7): 35. 1900. *Hookeriopsis leucomioides* (Broth.) Broth., Nat. Pflanzenfam. I(3): 939. 1907. Protologue. Paraguay: San Bernardino, in convalli umbrosa saxosa ([*Lindman*] *n. 647*). Type. Paraguay, San Bernardino, 10/10/1893. *Lindman 647* (H, holotype), *syn. nov*.

Plants small and slender, 1–2 cm long, yellowish green to green, in loose or dense mats. Stems prostrate, irregularly branched, whitish to yellowish when young, red with age, somewhat complanate-foliate; stems in cross section with 1–3 rows of somewhat small, firm-walled epidermal cells, cortical cells enlarged, firm-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2-celled, basal cell short-rectangular, reddish brown, upper cell oblong-elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions at base of costae, smooth, reddish brown, not or sparsely and irregularly branched. Leaves erect, erect-spreading, somewhat flattened, lightly contorted to twisted when dry, erect-spreading, flexuose when wet. Dorsal and lateral leaves lanceolate to ovate-lanceolate, 0.8–1.4 mm long, gradually acute to broadly acute; margins coarsely serrate to dentate in upper 2/3, teeth at times swollen and bifid, serrate to subentire below, plane to erect; costae double, ending 2/3–3/4 the leaf length, weakly diverging throughout or parallel, serrate on back, projecting at the apices; cells smooth, at times weakly prorate near apex, upper and median cells long-rectangular to elongate-fusiform, thin-walled, eporose, 30–60 × 4–6 µm, lower cells between the costae 30–50 × 4–6 µm; basal cells near the insertions enlarged, oblong-rectangular; alar cells short-rectangular, otherwise undifferentiated. Ventral leaves erect, ovate-lanceolate, symmetric; margins serrate in upper 2/3, teeth elongate, rarely bifid, entire below; costae double, slender, ending 2/3 the leaf length, diverging throughout, unequal, smooth on back, not projecting at the apices; upper cells elongate-flexuose. Autoicous. Setae elongate, 6–12 mm long, red, flexuose, smooth below, lightly papillose below capsules. Capsules inclined to pendent, short-cylindric, 1.0 mm long, neck well developed; exothecial cells quadrate to oblate in 2–3 rows at mouth, those below oblong to rectangular, thick-walled, collenchymatous; stomata rudimentary, 3–4-celled, on neck; opercula conic-rostrate, 0.5 mm long; annulus not seen; peristome diplolepideous, exostome narrowly triangular with broad median furrows, dorsal trabeculae projecting laterally, secondary walls on dorsal (outer) surface yellow above, red at base, densely and closely cross-striate below, coarsely papillose above, primary walls yellow, smooth, ventral (inner) surface hyaline to yellowish, deposition thin, lightly papillose;

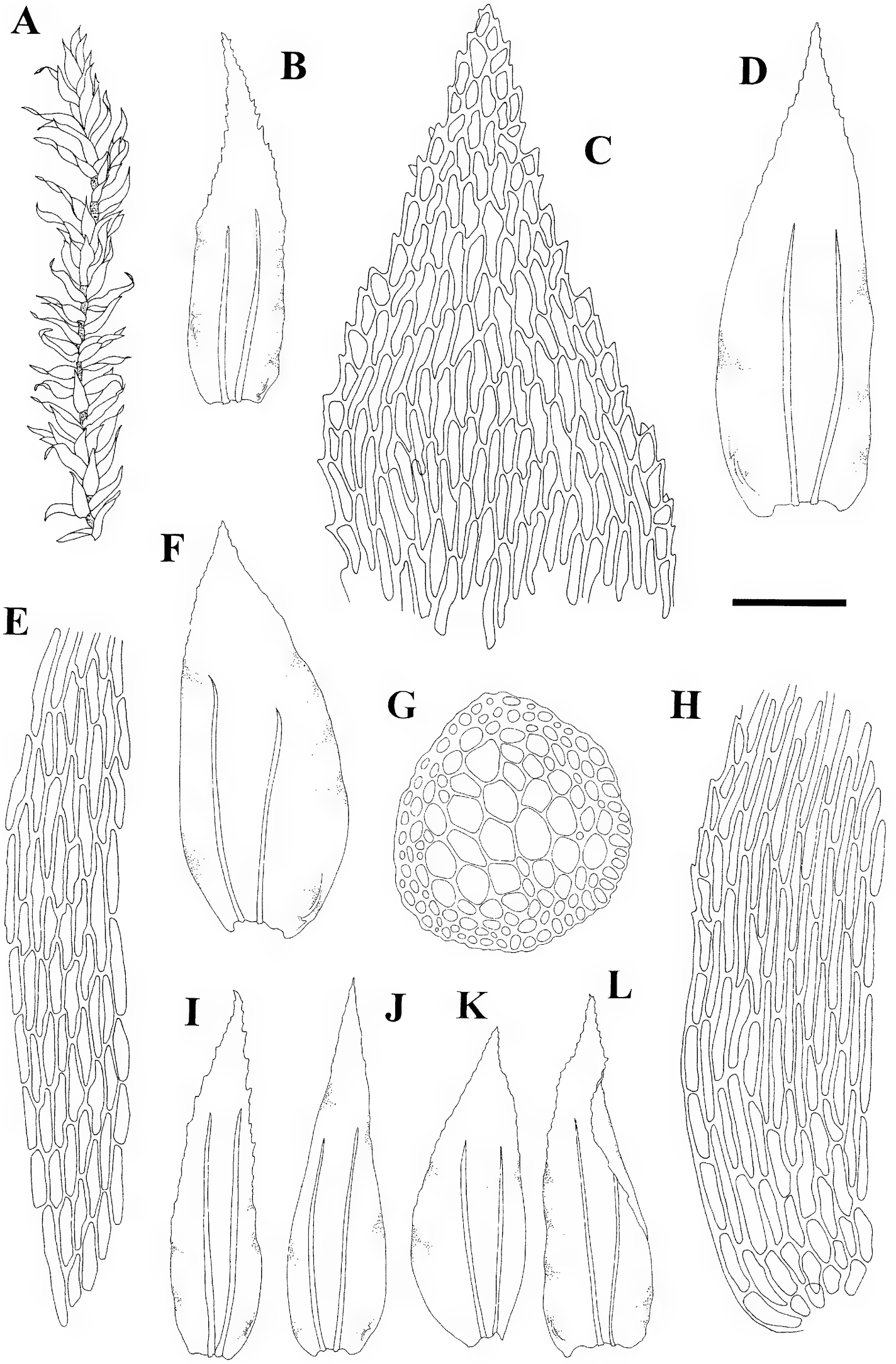
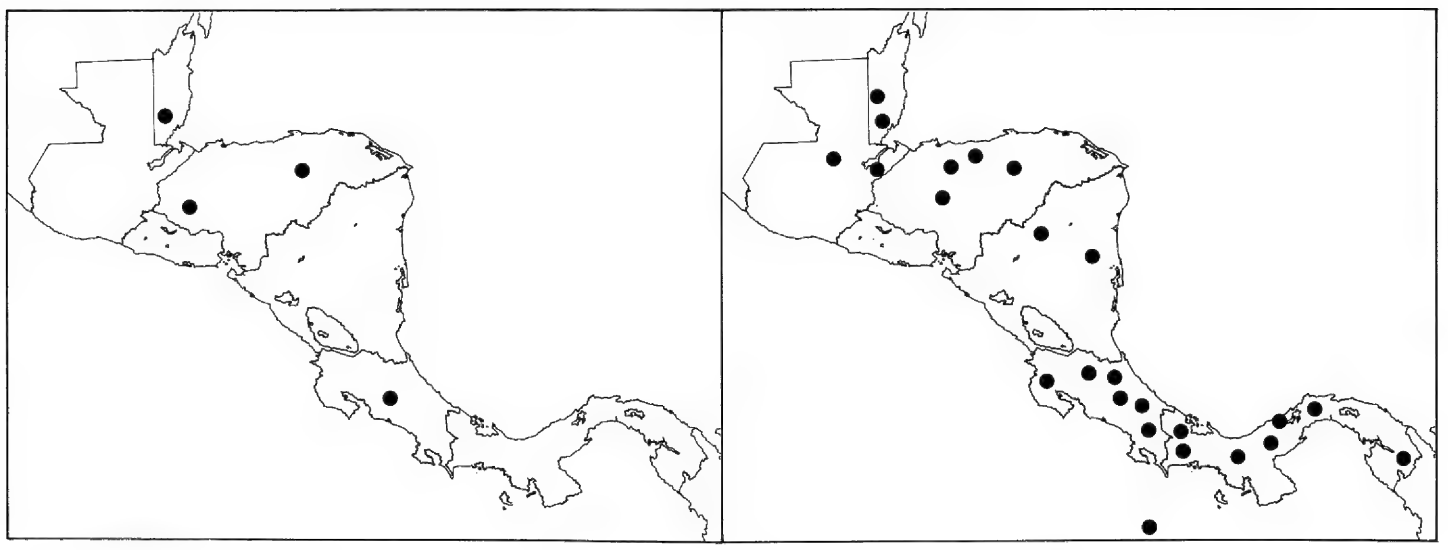


Figure 232. *Trachyxiphium variabile*. A. Habit. B, D, F & I–L. Leaves. C. Leaf apex. E. Median leaf cells between the costae. G. Stem in cross section. H. Basal and alar cells. Scale in mm: bar = 0.05 (C, E, H); bar = 0.08 (G); bar = 0.26 (B, D, F, I–L); bar = 1.56 (A). A, G from *Allen 12828*; B, C, E, H, L from *Garner* (type); D from *Spruce 641* (type *Hookeria tenuis*); F from *Lindman 647* (type *H. leucomioides*); I from *Puiggari 641b* (type *H. subaurescens*); J from *Glaziou 6354* (type *H. tenera*); K from *Glaziou 7152* (type *H. planiuscula*).



Trachyxiphium variabile *Leucomium strumosum*

endostome as long as the exostome, yellowish, lightly papillose throughout, basal membranes high, segments broad, strongly keeled, not perforate, cilia absent. Spores rounded, 10–12 µm, smooth to faintly roughened. Calyptrae mitrate, 1.0 mm long, yellowish white, red at times near apex, irregularly lobed at base, smooth or somewhat roughened, naked.

Illustrations. Vaz and Costa (2006a, Figs. 122–128). Figure 232.

Habitat. On rocks and decorticated logs in streams, and on rotting wood; 1000–2550 m.

Distribution in Central America. BELIZE. Toledo: *Allen 15493* (MO). HONDURAS. Lempira: *Allen 12047* (MO); Olancho: *Allen 12828* (MO). COSTA RICA. San José: *Crosby & Crosby 5986* (MO).

World range: Central America; Western, Northern, and Southern South America, Brazil.

Trachyxiphium variabile is a slender species with yellow green to green plants that have somewhat complanate-foliate stems and erect leaves that are shortly, at times broadly, acute. The leaf cells in *T. variabile* are homogeneously lax and fairly wide. The present treatment takes a broad view of the species in regard to leaf size and shape. The type of *T. variabile*, for example, has small, lanceolate leaves with marginal teeth often swollen and bifid, as do the types of *Hookeria planiuscula*, *H. subaurescens*, and *H. tenera.* Central American material of *T. variabile*, however, has larger, ovate-lanceolate leaves with mostly sharply serrate marginal teeth. This form of the species is identical to the types of *Hookeria leucomioides* and *H. tenuis*. The costae in *T. variabile* can be strong, with the dorsal surface sharply serrate with projecting tips, or weak and smooth on the dorsal surface. The sporophytes of *T. variabile* are small and slender, but otherwise typical for the Hookeriaceae.

In nearly all aspects *Trachyxiphium variabile* and *T. hypnaceum* are identical. They differ only in leaf apex shape: *T. variabile* with acute leaves; *T. hypnaceum* with long-acute to shortly acuminate leaves. The two species sometimes grow mixed, and further studies are needed to assess the range of variation found in each species. The two taxa may prove to be synonymous. Both species have a macroscopic aspect very similar to *Leucomium* or *Rhynchostegiopsis*, a resemblance reflected in the *Hookeria leucomioides* synonym of *T. variabile*. These genera differ from *T. variabile* in having ecostate leaves and cucullate calyptrae. *Leucomium* also has entire leaf margins.

LEUCOMIACEAE

Leucomiaceae Broth., Nat. Pflanzenfam. I(3): 1095. 1908.

Plants slender, medium-sized, or robust, pale green, whitish green, yellowish green, or reddish yellow, in loose or dense mats. Stems creeping to shortly ascending, sparsely and irregularly branched, at times complanate-foliate; stems in cross section with outer cells smaller than the inner cortical cells, otherwise undifferentiated, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs fragile, 2 cells long, basal cell short-rectangular, reddish brown, upper cell elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, not or sparsely and irregularly branched. Lateral and dorsal leaves flattened or erect-spreading, lanceolate to ovate, symmetric or asymmetric, apices broadly acute to acuminate; margins absolutely entire or sharply serrate to serrulate above; costa absolutely none; cells smooth, pellucid, lax, thin-walled, upper and median cells long-hexagonal to linear; basal cells enlarged, broadly long-rectangular; alar cells not differentiated. Ventral leaves lanceolate; margins smooth to weakly serrulate, marginal cells not bulgingly inflated; cells linear, narrow, firm-walled, otherwise similar to dorsal and lateral leaves. Asexual reproduction by gemmae clustered abaxial to the leaf insertions on leaf bases and contiguous stems; gemmae uniseriate, lightly minutely papillose. Synoicous, autoicous, or dioicous. Setae elongate, smooth. Capsules inclined, asymmetric, cylindric or ovoid-cylindric, neck well developed; exothecial cells with thick lateral walls, thick and thin horizontal walls, or collenchymatous; stomata on neck, variable in form: perfect, 2-celled and irregularly formed, 2–3-celled; opercula long-rostrate; annuli well developed, of several rows of thin-walled, quadrate cells, persistent at the base of the opercula; peristome diplolepideous; exostome teeth narrowly triangular, dorsal (outer) surface dark red, median furrows present, densely and closely cross-striate below, coarsely papillose above, ventral (inner) surface yellowish, smooth to lightly papillose, trabeculae weakly projecting; endostome as long as the exostome, yellowish, lightly papillose, basal membranes high, segments well developed, keeled, weakly perforate, cilia well developed, 1–2, rudimentary, or absent. Calyptrae cucullate or subcucullate, at times irregularly split at base, smooth, naked or sparsely hairy.

The Leucomiaceae (consisting of *Leucomium* and *Vesiculariopsis*) were originally positioned between the Hypnaceae and Sematophyllaceae (Brotherus 1908). Fleischer (1923) moved the family to the Hookeriales because of its gametophytic and sporophytic similarities to *Hookeria* and *Hookeriopsis*. At the same time he removed *Vesiculariopsis* from the family since it had a hypnaceous peristome. Robinson (1986) proposed that the Hookeriaceae-Leucomiaceae-Sematophyllaceae represented a related group linked by the ability to express three sporophytic character states: collenchymatous exothecial cells, furrowed exostome teeth, and long-rostrate opercula. Whittemore and Allen (1989), downplaying the importance of cucullate calyptrae as an indicator of family relationships, synonymized the Leucomiaceae with the Hookeriaceae; but the family has since been recognized by Buck and Goffinet (2000) and Goffinet and Buck (2004), who placed it next to the Hookeriaceae. There also appears to be strong molecular (Buck *et al.* 2005) support for the recognition of the Leucomiaceae.

The gametophytes of the Leucomiaceae are notable because they lack distinctive characters: stems internally undifferentiated; paraphyllia and pseudoparaphyllia absent; leaves ecostate and with alar cells undifferentiated. Characters that align the family with the Hookeriaceae include its 2-celled axillary hairs; long, smooth, very lax leaf cells; collenchymatous exothecial cells; irregularly formed stomata; well-developed, specialized annuli; and hookeriaceous exostome. It differs from the Hookeriaceae in having long-rostrate opercula; well-developed endostomial cilia in some genera; and cucullate calyptrae.

The Leucomiaceae consist of three loosely related genera: *Leucomium*, *Rhychostegiopsis*, and *Tetrastichium*. These genera share the following features: (1) internally undifferentiated stems; (2) no pseudoparaphyllia; (3) ecostate leaves with long, laxly bulging leaf cells; (4) cucullate calyptrae; (5) hookeriaceous exostome teeth with weak median furrows; (6) presence of well-developed or rudimentary endostomial cilia.

1. Leaf margins absolutely entire; plants synoicous or autoicous; endostomial cilia rudimentary or lacking . . . . . 1. *Leucomium*

1. Leaf margins sharply serrate or serrulate; plants dioicous; endostomial cilia 1–3, well developed. . . . . 2. *Rhynchostegiopsis*

1. *Leucomium* Mitt., J. Linn. Soc., Bot. 10: 181. 1868.

Plants small to medium-sized, pale green, whitish green, in loose or dense mats. Primary stems creeping, secondary stems horizontal to shortly ascending, sparsely or densely irregularly branched, at times complanate-foliate; in cross section stem cells homogenous, thin-walled throughout, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2 cells long, basal cell short-rectangular, reddish brown, upper cell elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, not or sparsely and irregularly branched. Leaves flattened, erect-spreading, or secund, variably dimorphic, ventral leaves narrowly lanceolate, lateral leaves oblong-lanceolate to triangularly lanceolate, dorsal leaves as in lateral leaves or ovate to oblong-ovate OR leaves uniformly oblong- to ovate-lanceolate, symmetric or asymmetric, apices flexuose-piliferous, long, narrowly acuminate, or long and broadly acute; margins absolutely entire, plane or inflexed on one side below, elimbate; costa none; cells smooth, pellucid, lax- or firm-walled, upper and median cells long-hexagonal, rhomboidal, or linear; basal cells enlarged, broadly long-rectangular; alar cells not differentiated. Asexual structures unknown. Synoicous, autoicous, or polyoicous. Setae elongate, smooth or roughened above. Capsules inclined asymmetric, ovoid to cylindric, neck well developed, often warty; exothecial cells collenchymatous; stomata rudimentary, 3–5-celled, on neck; opercula long-rostrate; annuli well developed, of 7–8 rows of thin-walled, quadrate cells, persistent at the base of the opercula; peristome diplolepideous; exostome teeth narrowly triangular, median furrows present, dorsal (outer) surface densely and closely cross-striate at base, ventral (inner) surface smooth to lightly papillose, trabeculae weakly projecting; endostome as long as the exostome, lightly papillose, basal membranes high, segments well developed, keeled, weakly perforate, cilia absent or rudimentary. Calyptrae cucullate, smooth, naked or sparsely hairy.

Leucomium is a genus of two species, one pantropical, the other restricted to the Guayana highlands of southeastern Venezuela and western Guyana. The genus is commonly found on rotting wood. Its plants usually have a very distinctive whitish green color, and the stems lack internal differentiation. The ovate-lanceolate to oblong-lanceolate (often dimorphic) leaves have narrowly acuminate to broadly acute apices; absolutely entire margins; smooth, very long, laxly bulging median leaf cells; enlarged, broadly long-rectangular basal cells; and undifferentiated alar cells. The leaves are absolutely ecostate. Sporophytically *Leucomium* has elongate setae and inclined capsules with collenchymatous exothecial cells, rudimentary stomata, a hookeriaceous peristome in which the median furrow is variably developed, and rudimentary to absent endostomial cilia. As in many Hookeriaceae genera, *Leucomium* has a specialized, massive annulus that consists of numerous rows of thin-walled, quadrate cells that are persistent at the base of the opercula. *Leucomium* has fully formed, cucullate calyptrae that are naked or sparsely hairy.

In Central America *Vesicularia* is often confused with *Leucomium* because they are similar in color and aspect, as well as leaf shape and areolation. Plants of *Vesicularia* are usually more regularly branched, and they have stems with weakly developed central strands, weakly serrulate leaf margins, and weak double costae. Most well-developed plants of *Vesicularia* can be separated from *Leucomium* on the basis of the above features, but not always. A distinctive feature of *Vesicularia*, and one that consistently separates it from *Leucomium*, is the presence of odd, filamentous pseudoparaphyllia that consist of short, bulging cells. Sporophytically *Vesicularia* differs from *Leucomium* in having conic opercula and endostomial cilia. *Leucomium* was revised by Allen (1987b).

The name *Leucomium* combines the Greek *leucon* (white color) with an orthographic variant of *mni* (moss), in reference to the whitish color of its plants.

Leucomium strumosum (Hornsch.) Mitt., J. Linn. Soc., Bot. 12: 502. 1869. *Hookeria strumosa* Hornsch., Fl. Bras. 1(2): 69. 1840. *Hypnum strumosum* (Hornsch.) Müll. Hal., Syn. Musc. Frond. 2: 238. 1851. *Acosta strumosa* (Hornsch.) Müll. Hal. *ex* Yano, Bol. Inst. Bot. (São Paulo) 10: 136. 1996, invalid combination. *Vesicularia strumosa* (Hornsch.) Yano, Bol. Inst. Bot. (São Paulo) 10: 136. 1996, invalid combination, basionym not cited. Protologue. [Brazil] In Serra dos Orgaôs

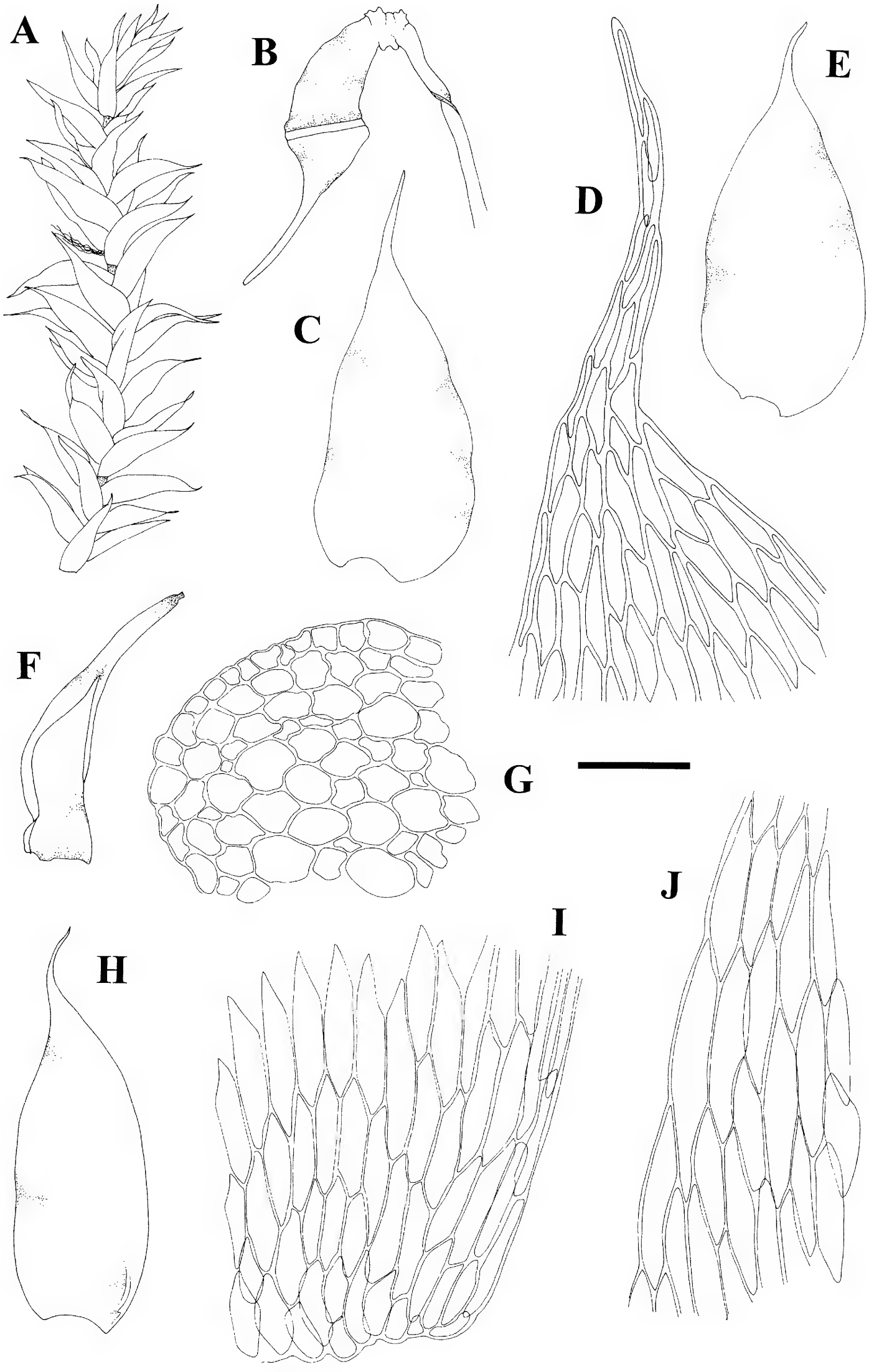


Figure 233. *Leucomium strumosum*. A. Habit. B. Seta, capsule, annulus, and operculum. C, E & H. Leaves. D. Leaf apex. F. Calyptra. G. Stem in cross section. I. Basal and alar cells. J. Upper leaf cells and margin. Scale in mm: bar = 0.13 (G, I, J); bar = 0.18 (D); bar = 0.6 (B, C, E, F, H); bar = 1.96 (A). B, F from *Folsom 6411*; all other figure parts from *Allen 18770*.

[sic], Februario, et prope Sebastianopolin, Octobri: *Beyrich*; —in lapidibus ibidem, Julio et Augusto, c.fr. maturis: *Merkel*; —prope Tijucam: *Olfers*. Type (see Allen 1987b). Prope Tijucam, *Olfers* (BM, lectotype).

Acosta cuspidata Müll. Hal., Linnaea 21: 192. 1848. *Hypnum cuspidatifolium* Müll. Hal., Syn. Musc. Frond. 2: 237. 1851, new name in *Hypnum*, not *Hypnum cuspidatum* Hedw., 1801. *Leucomium cuspidatifolium* (Müll. Hal.) Mitt., J. Linn. Soc., Bot. 12: 501. 1869. *Leucomium cuspidatum* (Müll. Hal.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1877–78: 275. 1879. Protologue. [Suriname] An faulen Baustämmen in den Wäldern bei Paramáribo. Juni und Juli mit unreifen Früchten; Februar (1844) mit reifen Capseln. Sehr haüfig. Hb. *Kegel. No. 990.* Type (see Allen 1987b). *Kegel*, Juli 1844 (GOET, lectotype).

Hypnum acrophyllum Hampe, Ann. Sci. Nat., Bot., sér. 5, 5: 325. 1866. *Leucomium acrophyllum* (Hampe) Mitt., J. Linn. Soc., Bot. 12: 501. 1869. Protologue. [Colombia] Bogotá, Pacho, 2000 m, in sylvis ligno adnatum, intermixtum parce legit julio 1863 *A. Lindig*. Types. *Lindig* (BM, holotype; NY, isotype).

Leucomium compressum Mitt., J. Linn. Soc., Bot. 12: 502. 1869. Protologue. Ins. Trinidad, *Black*. [Brazil] Fl. Negro, S. Gabriel ad truncos emortuos, *Spruce, n. 803b*; S. Carlos, *Spruce, n. 803d*; ad basin montis Cocui, *Spruce, n. 803g*. Andes Peruvianae, ad fl. Huallaga, in truncis, *Spruce, n. 803f*. Types (see Allen 1987b). Rio Negro, ad truncos emortuos, *Spruce 803b* (NY, lectotype; BM, FH, G, H, NY, isolectotypes).

Leucomium attenuatum Mitt., J. Linn. Soc., Bot. 12: 503. 1869. Protologue. Ins. Sti. [sic] Vincentis, *Guilding in Herb. Hooker.* Types. St. Vincent, *Guilding* (BM, holotype; BM, NY, isotypes).

Leucomium mariei Besch., J. Bot. (Morot) 8: 178. 1894. Protologue. Guadeloupe: bords de la rivière Duplessis, sur les troncs d'arbres, 26 novembre 1877. (*Ed. Marie, n^{os} 519, 527, 693*). Type (see Allen 1987b). *Marie 693* (BM, lectotype).

Leucomium mosenii Broth., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 21 Afd. 3(3): 56. 1895. Protologue. [Brazil] Prov. Minas Geraës, Caldas, in ripa umbrosa humida amnis Rio Capivary, ad terram (*Mosén n. 264*) et Caldas ad rivulos (*n. 394*). Types (see Allen 1987b). *Mosén 264* (H, lectotype; BM, NY, isolectotypes); *Mosén 394* (FH, H, syntypes).

Leucomium guianense Müll. Hal., Malpighia 10: 515. 1896. Protologue. [Guyana] [Marshall Falls on Mazaruni River near Georgetown, *Quelch*.] Types (see Allen 1987b). *Quelch* (BM, lectotype; NY, isotype).

Leucomium connexum Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 41(1): 113. 1905. Protologue. Hab. Antilles: Portorico (*A. Heller*). Types. *Heller* (H, MO, NY, isotypes).

Leucomium costaricense Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 41(1): 145. 1905. Protologue. [Costa Rica] Forêts à General (*Pitt.*[*ier*] n^{os} *5797*); forêts de Juan Viñas, [*Pittier*] n^{os} *5798* et *5799*). Types. Plantae costaricenses exsiccatae. H. Pittier & Th. Durand, Costa Rica. Forêts à General, Feb. 1891, *H. Pittier n^{o}5797* (US, syntype); Plantae costaricenses exsiccatae. H. Pittier & Th. Durand, Forêts de Juan Viñas, cum *no. 5732*, *Pittier n^{o}5799* (US, syntype), *syn. nov*.

Leucomium mouretii Thér. & Corb., Ann. Bryol. 7: 158. 1934. Protologue. Martinique: camp de Balata, sur troncs d'arbres; *Mouret*, 1913. Type. *Mouret s.n.* (H, isotype).

Leucomium scabrum Besch. *ex* Thér., Ann. Bryol. 7: 159. 1934. Protologue. Guadeloupe. Types (see Allen 1987b). Guadeloupe (NY, lectotype; G, isolectotype).

Leucomium latifolium E. B. Bartram, Bryologist 49: 120. 1946. Protologue. [Guatemala] Dept. Alta Verapaz: Cerro Chinaja, between Finca Yalpemech and Chinaja, above source of Río San Diego, alt. 150–700 m, *Steyermark 45668*. Type. Guatemala. Dept. Alta Verapaz: Cerro Chinaja, between Finca Yalpemech and Chinaja, above source of Río San Diego, alt. 150–700 m, *Steyermark 45668* (FH, holotype).

Leucomium robustum E. B. Bartram, Bull. Brit. Mus. (Nat. Hist.) Bot. 2: 47. 1955. Protologue. [Dominica] Morne Diablotin, windward slope, 760–900 m, [*Elliot*] *2204*. Types (see Allen 1987b). *Elliott 2204* (BM, holotype; FH, isotype).

Plants small to medium-sized, pale green, whitish green, in loose or dense mats. Primary stems creeping, secondary stems fragile, horizontal to shortly ascending, 2–3 cm long, sparsely or densely irregularly branched, hyaline to pale green, epidermal cells quadrate to short-rectangular, at times complanate-foliate; stems in cross section with cells homogeneous, thin-walled throughout, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs 2 cells long, basal cell short-rectangular, reddish brown, upper cell elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, not or sparsely and irregularly branched. Leaves flattened or erect-spreading, frequently secund, especially at the tips, densely foliate, 1–3 mm long, variably dimorphic, ventral leaves narrowly lanceolate, lateral leaves oblong-lanceolate to triangularly lanceolate, dorsal leaves as in lateral leaves or ovate to oblong-ovate OR leaves uniformly oblong- to ovate-lanceolate, symmetric or asymmetric; apices flexuose-piliferous, long, narrowly acuminate, or long and broadly acute; margins absolutely entire, plane or inflexed on one side below, elimbate; costa none; cells

smooth, pellucid, lax- or firm-walled, upper and median cells long-hexagonal, rhomboidal, or linear, 60–285 × 10–50 µm; basal cells enlarged, broadly long-rectangular; alar cells not differentiated. Synoicous, autoicous, or polyoicous. Setae elongate, 8–20 mm long, red to red brown, smooth below or throughout, at times roughened below capsules. Capsules pendent to erect-curved, asymmetric, ovoid to cylindric, 0.3–0.8 mm long, neck well developed, often warty; exothecial cells rounded to short-rectangular, collenchymatous; stomata rudimentary, 3–5-celled, on neck; opercula long-rostrate, 1.0 mm long; annuli well developed, of 7–8 rows of thin-walled, quadrate cells, persistent at the base of the opercula; peristome diplolepideous; exostome teeth narrowly triangular, dorsal (outer) surface dark red, median furrows present, densely and closely cross-striate below, coarsely papillose above, ventral (inner) surface hyaline to yellowish, smooth to lightly papillose, trabeculae weakly projecting; endostome as long as the exostome, yellowish, lightly papillose, basal membranes high, segments well developed, keeled, weakly perforate, cilia absent or rudimentary. Spores rounded, 10–18 µm, finely papillose. Calyptrae cucullate, 1.5–2.0 mm long, smooth, naked or with a few uniseriate, hyaline hairs.

Illustrations. Sullivant (1859, Pl. 21 B); Dozy and Molkenboer (1867, Pl. 282, as *Hypnum aneurodictyon*); Brotherus (1908, Fig. 775 A–E, as *L. aneurodictyon*; F, as *L. strumosum*); Fleischer (1923, Fig. 185, as *L. aneurodictyon*); Brotherus (1925, Fig. 623 A–E, as *L. aneurodictyon*; F, as *L. strumosum*); Potier de la Varde (1925, Fig. 17 as *L. letestui*); Potier de la Varde (1928, Fig. 29 as *L. letestui*); Potier de la Varde (1936, Fig. 52, as *L. letestui*); Bartram (1939, Pl. 20 351, as *L. aneurodictyon*); Bartram (1949, Fig. 144 C–E, as *L. lignicola*; F–H, as *L. latifolium*); Whittier (1976, Fig. 74 E–G, Fig. 75, as *L. aneurodictyon*); Churchill (1994, Fig. 26 A); Sharp *et al.* (1994, Fig. 628); Churchill and Linares (1995, Fig. 119 a & b); Veling (1996, Fig. 143); Duarte Bello (1997, Pl. 304, as *L. compressum*); Buck (1998, Pl. 36); Gradstein *et al.* (2001, Fig. 149 M & N); Buck (2003, Fig. 103). Figure 233.

Habitat. On rotting logs, fern fronds, soil, humus, roots, tree trunks, and rocks or boulders in the forest or along streams; 5–1800 m.

Distribution in Central America. BELIZE. Cayo: *Allen 18040* (BRH, MO); Toledo: *Allen 18770* (BRH, MO). GUATEMALA. Alta Verapaz: *Türckheim* (FH); Izabal: *Steyermark 39766* (FH). HONDURAS. Atlántida: *Allen 17475* (MO, TEFH); Comayagua: *Olson 84-37* (MO); Olancho: *Allen 12499* (MO); Yoro: *Allen 13470* (MO, TEFH). NICARAGUA. Jinotega: *Seymour 5881* (MO); Zelaya: *Stevens 16485* (HNMN, MO). COSTA RICA. Alajuela: *McQueen 5068* (MO); Cartago: *Standley 51080a* (FH); Guanacaste: *Alfaro 1a* (FH); Heredia: *Bowers 799-b* (MO); Limón: *Stevens 23866A* (MO); Puntarenas: *Koch 4974* (MO), Cocos Island: *Gómez 4604* (CR, MO). PANAMA. Bocas del Toro: *Allen 5666* (MO); Chiriquí: *Allen 5459* (MO); Coclé: *Crosby 4396* (MO, PMA); Colón: *Crosby 10360* (MO); Darién: *Allen 8895* (MO, PMA); Panamá: *Crosby 10100* (MO, PMA); Veraguas: *Mori & Kallunki 2652* (MO).

World range: Mexico; Central America; Caribbean; Western and Northern South America, Brazil; West, West-Central, East, and South Tropical Africa, Western Indian Ocean; Indian Subcontinent, Indo-China, Malesia; Southwestern and South-Central Pacific.

Leucomium strumosum is a small to medium-sized species that sometimes grows in mats, but often is found, especially on rotted wood, as scattered stems mixed with several other mosses. Its plants are pale to whitish green with complanate-foliate stems and erect-spreading leaves. The stems are light green to hyaline and, while the cells toward the center are somewhat larger than those at the margins, they otherwise lack internal differentiation. *Leucomium strumosum* has monomorphic or dimorphic, lanceolate or oblong-lanceolate, symmetric or asymmetric leaves with usually narrow acumina, and consistently entire margins. The leaves are absolutely ecostate and have smooth cells; broad or narrow long-hexagonal to linear upper cells; enlarged, broadly rectangular basal cells; and undifferentiated alar cells. The species is synoicous or autoicous, and the sporophytes are typically hookeriaceous: elongate setae; collenchymatous exothecial cells; rudimentary stomata; massive, persistent annulus; and hookeriaceous peristome. The calyptrae are cucullate and either naked or sparsely hairy.

In Central America *Leucomium strumosum* is most often confused with *Vesicularia vesicularis* because their plants are similar in color, with the same leaf shape and laxly bulging leaf cells. *Vesicularia vesicularis* differs from *L. strumosum* in having a weakly differentiated stem central strand,

usually weakly serrulate leaf margins, often weak double costae, distinctive filamentous pseudoparaphyllia, endostomial cilia, and conic opercula. At times, however, plants of *V. vesicularis* lack a stem central strand, have entire leaf margins, and have no discernable costae. When these collections also lack sporophytes they are very difficult to distinguish from *L. strumosum*. *Vesicularia vesicularis* consistently differs from *L. strumosum* in having filiform pseudoparaphyllia that consist of short, bulging cells.

Leucomium strumosum is stenotypic throughout much of its range, but in some parts of Central America, and especially in South America, the species is incredibly variable in plant aspect, leaf shape, cell length, and cell width. This variability has three distinct expressions that are distinguished in the following key.

1. Leaves dimorphic: dorsal leaves ovate to oblong-ovate, shortly acuminate, lateral and ventral leaves lanceolate to oblong-lanceolate, slenderly long-acuminate; plants complanate-foliate, leaves erect-spreading . . . . . *compressum*-expression
1. Leaves monomorphic; lanceolate to ovate-lanceolate, slenderly acuminate or ovate to oblong-ovate, shortly acuminate; plants weakly complanate-foliate or evenly foliate, leaves secund 2

2. Leaves lanceolate to ovate-lanceolate, slenderly acuminate; leaf cells laxly thin-walled, frequently bulging . . . . . *strumosum*-expression
2. Leaves ovate to oblong-ovate, shortly acuminate; leaf cells firm-walled or laxly thin-walled . . . . . *mosenii*-expression

2. *Rhynchostegiopsis* Müll. Hal., Nuovo Giorn. Bot. Ital., n.s., 4: 163. 1897.

Vesicularia (Müll. Hal.) Müll. Hal. sect. *Rhynchostegiopsis* Müll. Hal., Bull. Herb. Boissier 5: 211. 1897, invalid name, lacks a description.

Plants slender, medium-sized, or robust, pale green, yellowish green, or reddish yellow, in loose or dense mats, occasionally pendent. Stems creeping to shortly ascending, sparsely and irregularly branched, hyaline to pale green when young, red when old, epidermal cells long-rectangular or broadly rectangular, densely foliate or at times complanate-foliate; stems in cross section with cells weakly differentiated, outer cells smaller than the inner cortical cells, otherwise undifferentiated, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs fragile, 2 cells long, basal cell short-rectangular, reddish brown, upper cell elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, not or sparsely and irregularly branched. Lateral and dorsal leaves flattened or erect-spreading, lanceolate, oblong-lanceolate, ovate-lanceolate, ovate, symmetric or asymmetric, apices short- to long-acuminate, at times flexuose-piliferous; margins sharply serrate, serrulate to subentire above, plane or inflexed on one side below, marginal cells often enlarged and bulging; costa none; cells smooth, pellucid, lax, thin-walled, upper and median cells long-hexagonal to linear; basal cells enlarged, broadly long-rectangular; alar cells not differentiated. Ventral leaves lanceolate; margins smooth to weakly serrulate, marginal cells not bulgingly inflated; cells linear, narrow, firm-walled, otherwise similar to dorsal and lateral leaves. Asexual reproduction by gemmae from clusters of cells at extreme base of leaves and on stems contiguous with the leaf insertions or from modified rhizoidal initials; gemmae uniseriate, lightly minutely papillose. Dioicous. Setae elongate, smooth. Capsules inclined, asymmetric, cylindric or ovoid-cylindric, neck well developed; exothecial cells rectangular to long-rectangular, lateral walls thick, horizontal walls thin; stomata on neck, variable in form: perfect, 2-celled and irregularly formed, 2–3-celled; opercula long-rostrate; annuli well developed, of several rows of thin-walled, quadrate cells, persistent at the base of the operecula; peristome diplolepideous; exostome teeth narrowly triangular, dorsal (outer) surface dark red, median furrows present, densely and closely cross-striate below, coarsely papillose above, ventral (inner) surface yellowish, smooth to lightly papillose, trabeculae weakly projecting; endostome as long as the exostome, yellowish, lightly papillose, basal membranes high, segments well developed, keeled, weakly perforate, cilia 1–2, nodose. Calyptrae cucullate or subcucullate, at times irregularly split at base, smooth, naked.

Rhynchostegiopsis is a genus of five species restricted to the Neotropics. The genus is often found on rotting wood and is typically pale green in color, with stems that lack internal differentiation and lanceolate to ovate, often dimorphic leaves. Its leaves have gradually acuminate apices; sharply serrate to serrulate upper margins; smooth, very long, laxly bulging median leaf cells; enlarged, broadly long-rectangular basal cells; undifferentiated alar cells; and they are absolutely ecostate. Sporophytically, *Rhynchostegiopsis* has elongate setae and inclined capsules, with rectangular exothecial cells that have thickened vertical walls and 2-celled or rudimentary stomata. The peristome of *Rhynchostegiopsis* is essentially hookeriaceous, but the exostome has a narrow median furrow and the endostomial cilia are well developed. As in many Hookeriaceae genera, *Rhynchostegiopsis* has a specialized, massive annulus that consists of numerous rows of thin-walled, quadrate cells that are persistent at the base of the opercula. *Rhynchostegiopsis* has cucullate or subcucullate calyptrae that are often irregularly split at base.

In Central America *Rhynchostegiopsis* could be confused with *Vesicularia*, *Plagiothecium*, or *Ectropothecium*. All three genera differ from *Rhynchostegiopsis* in having leaves with short, double costae, smooth to serrulate leaf margins, and hypnaceous peristomes. Plants of *Vesicularia* also are more regularly branched than *Rhynchostegiopsis*; they have weakly developed central strands and filamentous pseudoparaphyllia. *Plagiothecium* further differs from *Rhynchostegiopsis* in having decurrent leaves with weakly serrulate leaf margins. *Ectropothecium* also differs in having leaves with a few inflated alar cells and internally differentiated stems. *Rhynchostegiopsis* was revised by Price (2001).

The name *Rhynchostegiopsis* combines the generic name *Rhynchostegium* with the Greek suffix *-opsis* (appearance of or looking like).

1. Plants robust, 3–10 cm long; leaves 3–6 mm long . . . . . 1. *R. carolae*
1. Plants small to medium-sized, 1–5 cm long; leaves 1.0–4.6 mm long 2

2. Leaves with gemmae borne on compact, erect groups of reddish brown filaments originating from dense clusters of short, quadrate cells at extreme base of dorsal or lateral leaves . . . . . 2. *R. costaricensis*
2. Leaves without gemmae or gemmae in loose greenish clusters on stems abaxial to the leaf insertions 3

3. Plants slender, leaves flexuose-contorted when dry, lanceolate to oblong-lanceolate . . . . . 3. *R. flexuosa*
3. Plants medium-sized, leaves smooth or faintly wrinkled when dry, ovate or ovate-lanceolate 4

4. Lateral leaves stiffly and smoothly complanate-secund with apices pointed downward toward the substrate, 1.0–2.5 mm long . . . . . 2. *R. costaricensis*
4. Lateral leaves loose, soft, erect-complanate, apices mostly horizontally projecting, 2.0–4.6 mm long . . . . . 4. *R. tunguraguana*

1. *Rhynchostegiopsis carolae* Crosby, Ann. Missouri Bot. Gard. 63: 373. 1976 [1977]. Protologue. Costa Rica. Prov. San José: Along Inter-American Highway, 13 km SE of El Empalme, 9.40 N, 83.51 W, 2600 m, *Marshall R. & Carol A. Crosby 5836*. Type. Costa Rica. San José: Along Inter American Highway. 13 km SE of El Empalme. Oak Forest. 2600 m altitude. 9.40 N, 83.51 W. 15.iii.1973, *Marshall R. & Carol A. Crosby 5836* (MO, holotype).

Plants robust, pale green to yellowish green, in loose mats. Stems creeping to shortly ascending, 3–10 cm long, sparsely and irregularly branched, hyaline to pale green when young, red when old, epidermal cells long-rectangular to elongate, densely and often complanate-foliate; stems in cross section stems with cells weakly differentiated, outer cells smaller and more thick-walled than the inner cortical cells, central strand absent; paraphyllia absent; pseudoparaphyllia absent, scale leaves present; axillary hairs fragile, 2 cells long, basal cell short-rectangular, reddish brown, upper cell elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, not or sparsely and irregularly branched. Leaves flattened or erect-spreading, 3–6 mm long, dorsal leaves narrower than lateral leaves, otherwise leaves similar, ovate-lanceolate, symmetric or asymmetric, apices flexuose-piliferous to long, narrowly acuminate; margins serrulate to subentire above, plane or

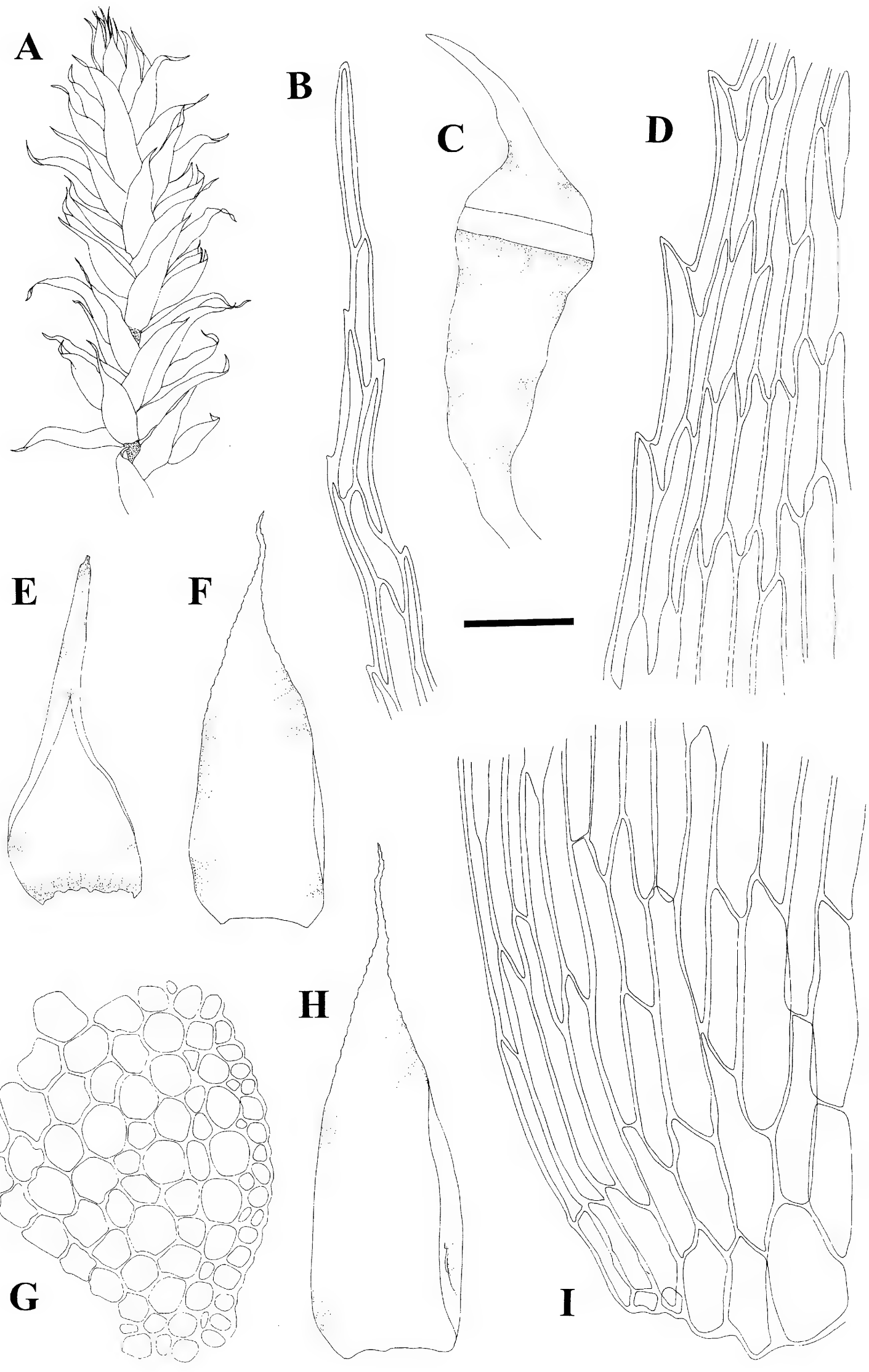
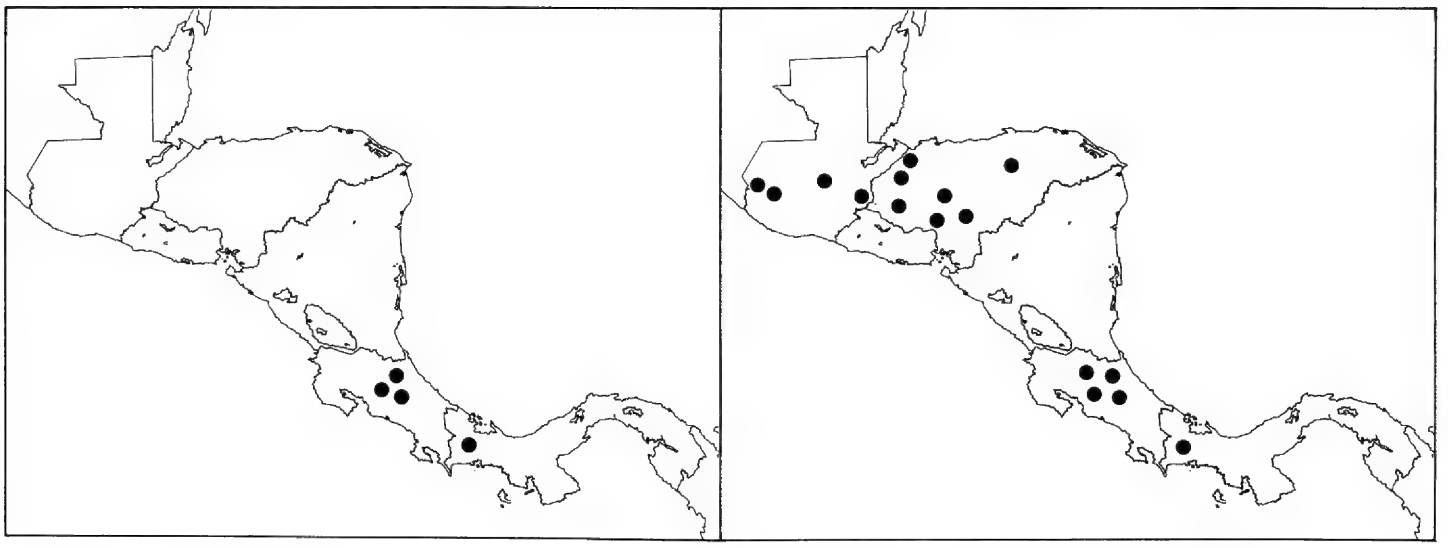


Figure 234. *Rhynchostegiopsis carolae*. A. Habit. B. Leaf apex. C. Seta, capsule, annulus, and operculum. D. Upper leaf cells and margin. E. Calyptra. F & H. Leaves. G. Stem in cross section. I. Basal and alar cells. Scale in mm: bar = 0.09 (B, D, I); bar = 0.17 (G); bar = 0.6 (C); bar = 1.25 (F, H); bar = 1.3 (E); bar = 4.0 (A). A, C, E from *Crosby 9766*; all other figure parts from *Crosby & Crosby 5836* (type).



Rhynchostegiopsis carolae *Rhynchostegiopsis costaricensis*

inflexed on one side below, elimbate, absolutely ecostate; cells smooth, pellucid, lax, thin-walled, upper and median cells long-hexagonal to linear, 100–290 × 10–27 µm; basal cells enlarged, broadly long-rectangular; alar cells not differentiated. Dioicous. Setae elongate, 15–40 mm long, red to red brown, smooth. Capsules inclined, asymmetric, cylindric, 1.5–2.0 mm long, neck well developed; exothecial cells rectangular to long-rectangular, lateral walls very thick, horizontal walls thin; stomata on neck, variable in form: perfect, 2-celled and irregularly formed, 2–3-celled; opercula long-rostrate, 1.5 mm long; annuli well developed, of 7–8 rows of thin-walled, quadrate cells, persistent at the base of the opercula; peristome diplolepideous; exostome teeth narrowly triangular, dorsal (outer) surface dark red, median furrows present, densely and closely cross-striate below, coarsely papillose above, ventral (inner) surface yellowish, smooth to lightly papillose, trabeculae weakly projecting; endostome as long as the exostome, yellowish, lightly papillose, basal membranes high, segments well developed, keeled, weakly perforate, cilia 1–2, nodose. Spores rounded, 12–18 µm, smooth to finely papillose. Calyptrae cucullate, 2.0 mm long, smooth, naked.

Illustrations. Crosby (1976, Figs. 1–7); Price (2001, Fig. 5). Figure 234.

Habitat. On moist ground, shaded banks, drainage ditches, and on tree trunks; 1400–3050 m.

Distribution in Central America. COSTA RICA. Cartago: *Crosby & Crosby 5957* (MO); Heredia: *Crosby 3704* (CR, FH, MO); San José: *Crosby 10861* (CR, FH, MO, PMA). PANAMA. Chiriquí: *Antonio 1432* (MO).

World range: Central America.

Rhynchostegiopsis carolae is a robust, pale green to yellowish green species that grows in large, loose mats. Its stems are sparsely to irregularly branched, more or less undifferentiated internally, and they have complanate-foliate stems with erect-spreading leaves. Its ovate-lanceolate leaves have piliferous to long, narrowly acuminate apices; serrate to serrulate upper margins with the marginal cells not distinctly enlarged; long-hexagonal or linear (to 290 µm long) upper leaf cells; enlarged, broadly rectangular basal cells; undifferentiated alar cells; and they are absolutely ecostate. The species is dioicous, and sporophytes are not commonly encountered. Its sporophytes have elongate setae, exothecial cells with very thick vertical walls, both 2-celled and 3–4-celled rudimentary stomata, and a large, persistent annulus. The peristome in *R. carolae* has endostomial cilia; otherwise it is a typical hookeriaceous peristome. The calyptrae are cucullate and naked.

In Central America *Rhynchostegiopsis carolae* differs from all other *Rhynchostegiopsis* species in its exceptionally large plant and leaf size. Price (2001) indicated that some collections of *R. tunguraguana* approached the size of *R. carolae*, but that species differs from *R. carolae* in having narrower leaves (0.7–1.6 mm vs. 1.5–2.1 mm wide, Price 2001), more crowded, falcate leaves, and distinctly enlarged, bulging upper marginal leaf cells.

2. *Rhynchostegiopsis costaricensis* H. Rob. & D. G. Griffin, Phytologia 30: 281. 1975. Protologue. Costa Rica: Alajuela: Parque Nacional Volcán Poás, *Clusia* forest, east rim of crater. Plants on downed log. alt. 2450 m, 3 Sept. 1973. *D. Griffin 92*. Type. Plants of Costa Rica. Prov. Alajuela: Parque Nacional Volcán Poás, *Clusia* forest, east rim of crater. Plants on downed log. alt. 2450 m, 3 Sept. 1973. *D. Griffin III, 92*. (US, holotype).

Plants medium-sized, pale green, shiny yellowish green, or reddish yellow, in loose or dense mats. Stems creeping, to shortly ascending, 1–4 cm long, sparsely and irregularly branched, hyaline to pale green when young, red when old, epidermal cells long-rectangular to elongate, stiffly, densely complanate-foliate; stems in cross section with outer cells smaller and slightly thicker-walled than the inner cortical cells, otherwise cells undifferentiated, central strand absent; paraphyllia absent; pseudoparaphyllia absent, scale leaves present; axillary hairs fragile, 2 cells long, basal cell short-rectangular, reddish brown, upper cell elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, not or sparsely and irregularly branched. Leaves flattened, 1–2.5 mm long, lateral leaves ovate-lanceolate, symmetric or slightly asymmetric, apices short- to long-acuminate; margins serrate to serrulate, plane or inflexed on one side below, cells often enlarged and inflated forming border; costa none; cells smooth, pellucid, lax, thin-walled, upper and median cells long-hexagonal to linear, 90–150 × 8–15 µm; basal cells enlarged, broadly long-rectangular, extreme basal cells at middle of insertion line often greatly enlarged; alar cells not differentiated. Asexual reproduction by specialized structures originating from dense clusters of small, bulging, quadrate cells at extreme base of leaves and on stems contiguous to the leaf insertions; gemmae green to hyaline, uniseriate, borne terminally on compact, erect groups of reddish brown filaments. Dioicous. Setae elongate, 10–25 mm long, red to dark red, smooth. Capsules inclined, ovoid-cylindric, 1–2 mm long; exothecial cells rectangular to long-rectangular, lateral walls very thick, horizontal walls thin; stomata on neck, variable in form: perfect, 2-celled and irregularly formed, 2–3-celled; opercula long-rostrate, 1.2 mm long; annuli well developed, of 5–7 rows of thin-walled, quadrate cells, persistent at the base of the opercula; peristome diplolepideous; exostome teeth narrowly triangular, dorsal (outer) surface reddish yellow to red, densely and closely cross-striate below, coarsely papillose above, median furrows narrow, ventral (inner) surface yellowish, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose, basal membranes high, segments well developed, keeled, weakly perforate, cilia 1–2. Spores round, 10–14 µm, smooth to lightly minutely papillose. Calyptrae subcucullate, 3 mm long, irregularly split at base, naked.

Illustrations. Robinson and Griffin (1975, Figs. 1–9); Price (2001, Fig. 6). Figure 235.

Habitat. On humus, stream banks, rotting wood, or twigs; 1830–3130 m.

Distribution in Central America. GUATEMALA. Baja Verapaz: *Sharp 2766* (FH); Chiquimula: *Steyermark 31009* (FH); Quetzaltenango: *Standley 67450* (FH); San Marcos: *Sharp 5372* (FH, MO). HONDURAS. Comayagua: *Liesner 26810* (MO, TEFH); Cortés: *Allen 14206* (MO, TEFH); Francisco Morazán: *Allen 12363* (MO); La Paz: *Liesner 26479* (MO, TEFH); Lempira: *Allen 12112* (MO, TEFH); Olancho: *Allen 12670* (MO, TEFH); Santa Bárbara: *Allen 11615* (MO, TEFH). COSTA RICA. Alajuela: *Griffin & Araya 81* (MO); Cartago: *Crosby 9789* (FH, MO); Heredia: *Crosby 13128* (MO); San José: *Crosby & Crosby 6117* (MO). PANAMA. Chiriquí: *Crosby 3989* (MO).

World range: Central America.

Rhynchostegiopsis costaricensis is a medium-sized species with internally undifferentiated stems. Its ovate-lanceolate leaves are stiffly and smoothly complanate-secund with variously acuminate apices that project downward toward the substrate. The upper margins are serrate to serrulate and often have enlarged, bulging marginal cells. Its leaf cells are long-hexagonal to linear and smooth. The basal cells are enlarged, broadly rectangular at base, and often the extreme basal cells at the middle of the insertion line are greatly enlarged (see Fig. 619, Brotherus 1925). The alar cells are undifferentiated.

The outstanding feature of *R. costaricensis* is the presence of specialized asexual structures that occur at the extreme base of the dorsal and some lateral leaves. These asexual structures originate from dense clusters of small, bulging, quadrate cells. Similar dense clusters of cells have been observed at the leaf bases of *R. carolae*, but that species does not appear to have gemmae. The bulging

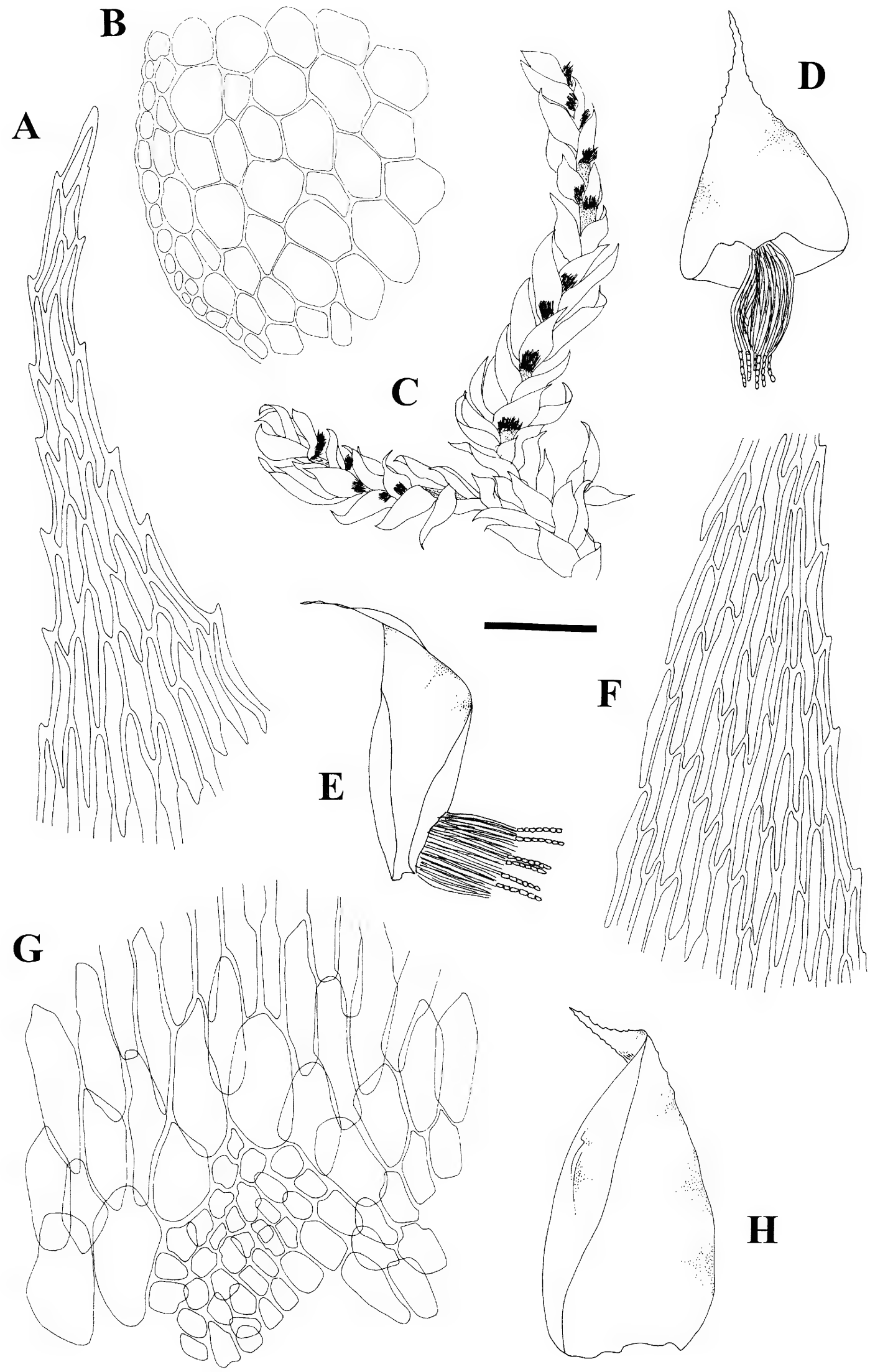


Figure 235. *Rhynchostegiopsis costaricensis*. A. Leaf apex. B. Stem in cross section. C. Habit. D, E & H. Leaves. F. Upper leaf cells and margin. G. Basal leaf cells at leaf insertion line showing gemmae initials. Scale in mm: bar = 0.06 (A, F, G); bar = 0.13 (B); bar = 0.5 (D, E, H); bar = 1.96 (C). All figure parts from *Crosby 13128*.

clusters of initials appear to arise at the extreme base of the leaves and from stem cells that are contiguous to the leaf insertions. In the former case the initials seem to be associated with the small area of enlarged bulging basal leaf cells noted above, but in the latter case the initials appear to be homologous to rhizoidal initials. Robinson and Griffin (1975) and Price (2001) attributed the origin of the asexual structures entirely to the enlarged basal cells, but these cells are very much different from the clusters of small cells that actually give rise to the gemmae. The asexual structures are stout, visible with a hand lens, and consist of dense clusters of erect, reddish filaments and terminal clusters of greenish to hyaline, uniseriate gemmae. Asexual gemmae occasionally occur in collections of *R. flexuosa* and *R. tunguraguana*, but in these species the gemmae form loose clusters and are strictly associated with transformed rhizoidal initials on the stems immediately abaxial to the leaf insertions. Curiously there are two species of *Cyclodictyon* (*C. richardsii* and *C. crosbyi*) that have asexual structures identical to those of *R. costaricense*.

In Central America *Rhynchostegiopsis costaricensis* is distinguished from all other *Rhynchostegiopsis* species by its specialized gemmae. In the absence of these structures, though, it can be difficult to distinguish from *R. flexuosa* or *R. tunguraguana.* The important features that separate it from these species are its medium plant size, ovate-lanceolate leaves, and most especially its leaf aspect. As noted above, in *R. costaricensis* the lateral leaves are stiffly and smoothly complanate-secund with the apices pointing downward toward the substrate. *Rhynchostegiopsis flexuosa* is a smaller, more slender species than *R. costaricensis*, and its lanceolate leaves are flexuose-contorted when dry. *Rhynchostegiopsis tunguraguana* is a somewhat larger species (leaves 1.7–4.6 mm vs. 1.0–2.5 mm long) than *R. costaricensis*, and its leaves are softly erect-complanate.

3. *Rhynchostegiopsis flexuosa* (Sull.) Müll. Hal., Nuovo Giorn. Bot. Ital. n.s. 4: 163. 1897. *Hypnum flexuosum* Sull., Proc. Amer. Acad. Arts 5: 288. 1861. *Leucomium flexuosum* (Sull.) Mitt., J. Linn. Soc., Bot. 12: 501. 1869. Protologue. Cuba. On dead wood, [*Charles Wright*] *112.*

Rhynchostegium cupressinum Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 250. 1872. *Rhynchostegiopsis cupressina* (Besch.) Cardot, Rev. Bryol. 38: 104. 1911. Protologue. [Mexico] Cordova (*Sallé* in herb. Decaisne).

Vescicularia auricolor Müll. Hal., Bull. Herb. Boissier 5: 211. 1897. *Rhynchostegiopsis auricolor* (Müll. Hal.) Broth., Nat. Pflanzenfam. (ed. 2) 11: 263. 1925. Protologue. [Guatemala] Pansamalá, 3800 ped. alta, Januar. 1886: *H. v. Türckheim* in Hb. Brotheri.

Plants small to medium-sized, pale green to yellowish green, in loose or dense mats. Stems creeping to shortly ascending, 1–4 cm long, sparsely and irregularly branched, hyaline to pale green when young, red when old, epidermal cells short, broadly rectangular, densely foliate or at times complanate-foliate; stems in cross section with outer cells somewhat smaller than the inner cortical cells, otherwise cells undifferentiated, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs fragile, 2 cells long, basal cell short-rectangular, reddish brown, upper cell elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, not or sparsely and irregularly branched. Lateral and dorsal leaves flexuose-contorted when dry, flattened, spreading, erect-spreading, or falcate to falcate-secund, lanceolate to oblong-lanceolate, 1–2 mm long, symmetric or asymmetric, apices long-acuminate; margins sharply serrate to serrulate above, plane or inflexed on one side below, marginal cells enlarged and bulging, sometimes forming a distinct border; costa absent; cells smooth, pellucid, lax, thin-walled, upper and median cells long-hexagonal to linear, 90–150 × 8–20 μm; basal cells enlarged, broadly long-rectangular, extreme basal cells at middle of insertion line often greatly enlarged; alar cells not differentiated. Ventral leaves lanceolate; margins smooth to weakly serrulate, marginal cells not bulgingly inflated; upper cells linear, narrow, firm-walled, otherwise similar to those of dorsal and lateral leaves. Asexual reproduction from gemmae in loose clusters on stems abaxial to the leaf insertions; gemmae green to hyaline, uniseriate, borne terminally on loose filaments. Dioicous. Setae elongate, 10–25 mm long, red to dark red, smooth. Capsules inclined, cylindric, 1–2 mm long; exothecial cells rectangular to long-rectangular, lateral walls very thick, horizontal walls thin; stomata on neck, variable in form: perfect, 2-celled and irregularly formed, 2–3-celled; opercula long-rostrate, 1 mm long; annuli well developed, of 3–5 rows of thin-walled, quadrate cells, persistent at the base of the opercula; peristome diplolepideous; exostome teeth narrowly triangular,

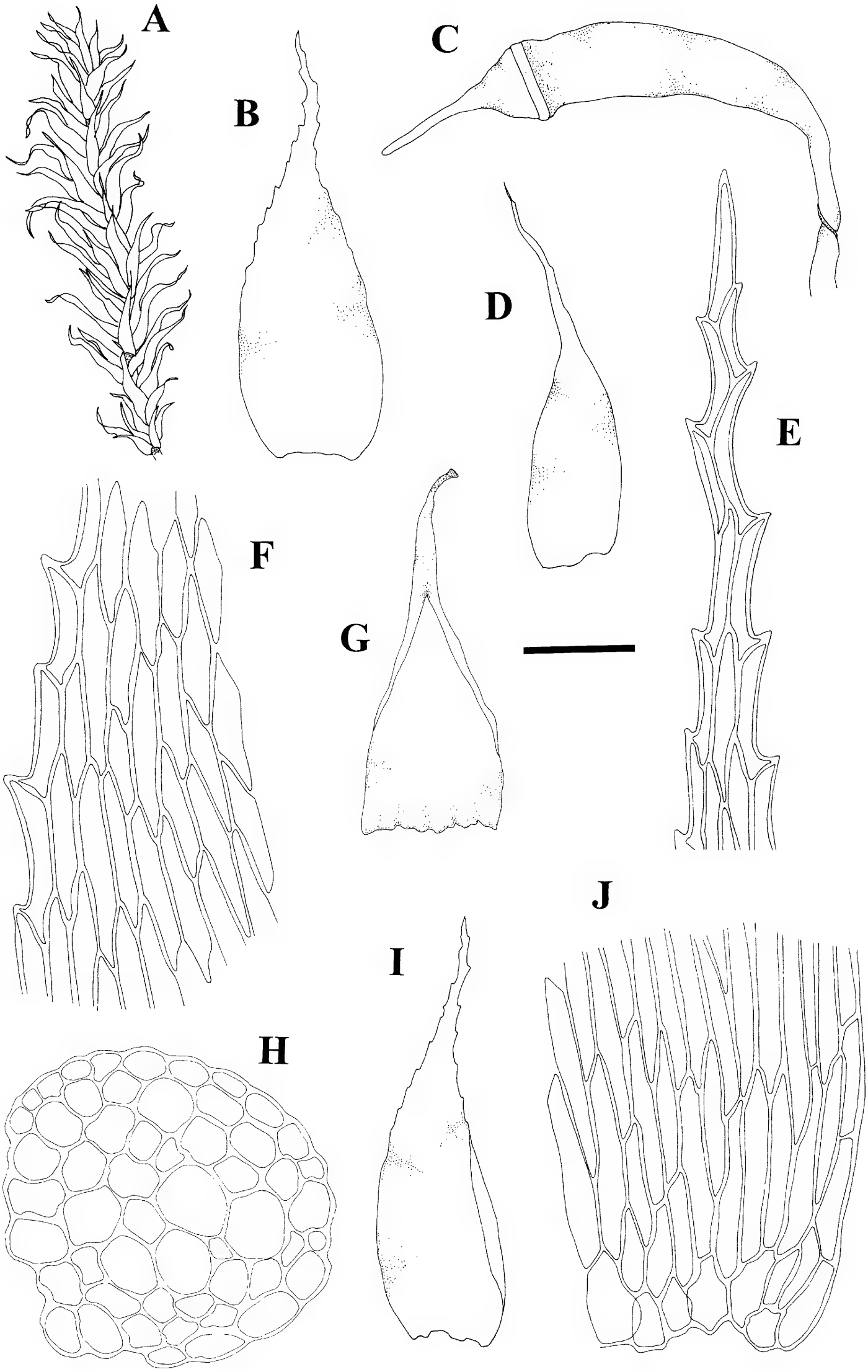
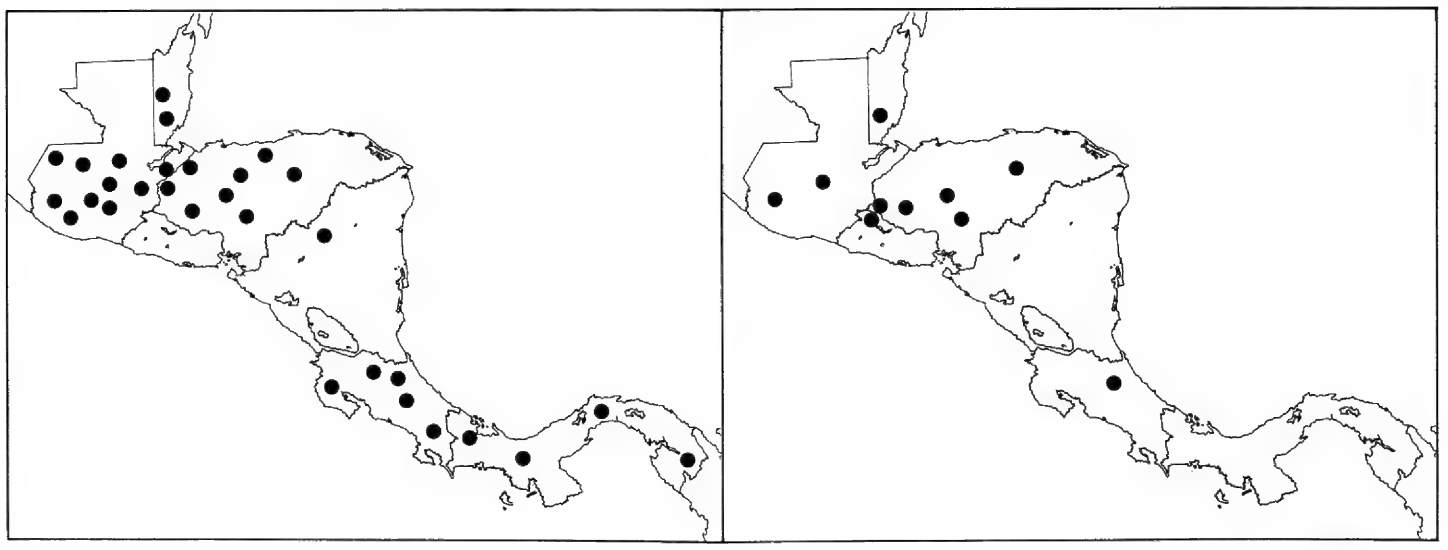


Figure 236. *Rhynchostegiopsis flexuosa*. A. Habit. B. Dorsal leaf. C. Seta, capsule, annulus, and operculum. D. Ventral leaf. E. Leaf apex. F. Upper leaf cells and margin. G. Calyptra. H. Stem in cross section. I. Lateral leaf. J. Basal and alar cells. Scale in mm: bar = 0.09 (E, F, J); bar = 0.08 (H); bar = 0.4 (B, D, I); bar = 0.6 (G); bar = 0.7 (C); bar = 1.56 (A). C from *Allen 11392*; G from *Allen 15464*; E, F, J from *Allen 5542*; all other figure parts from *Allen 15479*.



Rhynchostegiopsis flexuosa *Rhynchostegiopsis tunguraguana*

dorsal (outer) surface reddish orange, densely and closely cross-striate below, coarsely papillose above, median furrows narrow, ventral (inner) surface yellowish, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose, basal membranes high, segments well developed, keeled, weakly perforate, cilia 1–2, nodose. Spores round, 10–14 µm, smooth to lightly minutely papillose. Calyptrae cucullate, 2 mm long, naked.

Illustrations. Bartram (1949, Fig. 143 A–D); Welch (1966, Figs. 288–292); Welch (1972a, Figs. 261–267, as *R. serrata* (Besch.) Broth.); Sharp *et al.* (1994, Fig. 629); Duarte Bello (1997, Pl. 252); Buck (1998, Pl. 37 1–7); Price (2001, Fig. 7). Figure 236.

Habitat. On roots, tree trunks, moist ground, and decorticated or rotting logs, vines, and sticks, occasionally on rocks; 300–2850 m.

Distribution in Central America. BELIZE. Cayo: *Allen 15122* (BRH, MO); Toledo: *Allen 19006* (BRH, MO). GUATEMALA. Alta Verapaz: *Johnson 794* (US); Baja Verapaz: *Croat 41305* (MO); Chimaltenango: *Standley 61818* (MO); Guatemala: *Standley 80525* (FH); Huehuetenango: *Steyermark 48866* (MO); Izabal: *Steyermark 41919* (FH); Quetzaltenango: *Crosby 2840A* (FH, MO); Quiché: *Sharp 2506* (FH); Suchitepéquez: *Steyermark 46711* (FH); Zacapa: *Steyermark 42656* (FH). EL SAVADOR. Santa Ana: *Watson 77-01* (MO). HONDURAS. Atlántida: *Allen 17581* (MO, TEFH); Comayagua: *Allen 13792* (MO, TEFH); Copán: *Allen 17768* (MO); Cortés: *Allen 14198* (MO, TEFH); Francisco Morazán: *Allen 12369* (MO, TEFH); Lempira: *Allen 11925* (MO, TEFH); Olancho: *Allen 12497* (MO, TEFH); Yoro: *13618* (MO). NICARAGUA. Jinotega: *Stevens & Grijalva 15265* (HNMN, MO). COSTA RICA. Alajuela: *Dauphin & Valdelomar 2412* (MO); Cartago: *King C91-91* (MO); Guanacaste: *Chávez 73* (FH, MO); Heredia: *Crosby 9928* (MO); Puntarenas: *Lyon 28* (CR, MO). PANAMA. Bocas del Toro: *Allen 5542* (MO); Darién: *Allen 8843* (MO); Panamá: *Crosby 10109* (MO); Veraguas: *Crosby 10300* (MO).

World range: Mexico; Central America; Caribbean; Western South America.

Rhynchostegiopsis flexuosa is a small to medium-sized species with slender, lanceolate to oblong-lanceolate, long-acuminate leaves that are falcate to falcate-secund and typically flexuose-contorted when dry. In aspect *R. flexuosa* is identical to *Leucomium strumosum* but differs from it in having sharply serrate to serrulate upper leaf margins, with the marginal cells considerably enlarged and bulging. The stems of *R. flexuosa* lack internal differentiation. Its leaf cells are long-hexagonal to linear and smooth. The basal cells are enlarged, broadly rectangular at base, and often the extreme basal cells at middle of the insertion line are greatly enlarged. The alar cells are undifferentiated.

At times collections of *R. flexuosa* (*e.g.*, *Allen 11309*, MO) have gemmae that occur in loose clusters on the stems abaxial to the leaf insertions. The initials that give rise to the gemmae are identical in form and position to the rhizoidal initials of *R. flexuosa*, indicating the two structures may be homologous. Asexual gemmae also occur in *R. costaricensis* and *R. tunguraguana*. Those of the latter are identical in form and position to those of *R. flexuosa*, but in *R. costaricensis* they occur at the ex-

treme base of the dorsal and some lateral leaves. The gemmae in *R. costaricensis* originate from clusters of small, quadrate cells that arise at the extreme base of the leaves and from stem cells that are contiguous to the leaf insertions.

In Central America *Rhynchostegiopsis flexuosa* is distinguished from all other *Rhynchostegiopsis* species by its small plant size and slender, typically lanceolate leaves. In addition, *R. flexuosa* is often found at low elevations, while the other species are almost always found above 1800 meters. High elevation collections of *R. flexuosa*, however, approach *R. costaricensis* and *R. tunguraguana* in size. *Rhynchostegiopsis costaricensis* differs from large collections of *R. flexuosa* in having ovate-lanceolate leaves, the lateral ones stiffly, smoothly complanate-secund with the apices pointing downward toward the substrate. *Rhynchostegiopsis tunguraguana* differs from large forms of *R. flexuosa* in having larger, softly erect-complanate leaves (1.7–4.6 mm vs. 1–2 mm long). *Vesicularia vesicularis* can be confused with *R. flexuosa* because they have similarly shaped leaves with large, laxly bulging cells. *Vesicularia vesicularis* differs from *R. flexuosa* in having subpinnately to pinnately branched stems, bulging, lanceolate pseudoparaphyllia, and leaves that typically have short, double costae as well as weakly serrate upper marginal leaf cells that are not enlarged or bulging.

4. *Rhynchostegiopsis tunguraguana* (Mitt.) Broth., Nat. Pflanzenfam. I(3): 1235. 1909. *Stereodon tunguraguanus* Mitt., J. Linn. Soc., Bot. 12: 534. 1869. Protologue. [Ecuador] Andes Quitenses, in monte Tunguragua supra pagum Puela (6000 ped.), *Spruce, n 1048*. Type. Tunguragua, *Spruce 1048* (FH, isotype).

Rhynchostegiopsis complanata Müll. Hal., Nuovo Giorn. Bot. Ital. n.s. 4: 163. 1897. Protologue. Bolivia, collector not cited. Type (see Price 2001). Bolivia, Cochabamba: prope Choquecamata, June 1889, *Germain 1147* (NY, lectotype).

Rhynchostegiopsis lutescens E. Britton *in* Broth., Nat. Pflanzenfam. (ed. 2) 11: 263. 1925. Protologue. Jamaika, collector not cited. Type. Jamaica. St. Andrew: Slopes of Sir John and summit, Blue Mountains, 5 Oct. 1908, *Britton 1142* (NY, holotype).

Rhynchostegiopsis planifolia H. A. Crum & E. B. Bartram, Bull. Inst. Jamaica 8: 55. 1958, illegitimate name, includes species with priority. Based on: [Jamaica] St. Thomas: Terrestrial, moist bank in montane rain forest, 6000 ft. alt., Blue Mt. Peak track, *R. G. Robbins 89*, Dec. 16, 1951. Jamaica: Blue Mt. Peak track. Moist bank in Montane Rain forest at 6000 ft. Terrestrial. *R. G. Robbins, No. 89*. December 16, 1951 (US).

Plants medium-sized, shiny, pale green to yellowish green, in loose or dense mats, occasionally pendent. Stems creeping, to shortly ascending, 2–5 cm long, sparsely and irregularly branched, hyaline to pale green when young, red when old, epidermal cells broadly rectangular, densely or laxly complanate-foliate; stems in cross section with outer cells somewhat smaller than the inner cortical cells, otherwise cells undifferentiated, central strand absent; paraphyllia absent; pseudoparaphyllia absent; axillary hairs fragile, 2 cells long, basal cell short-rectangular, reddish brown, upper cell elongate, hyaline; rhizoids from clusters of initials abaxial to the leaf insertions, smooth, not or sparsely and irregularly branched. Lateral and dorsal leaves flattened, laxly spreading, falcate or erect, ovate to ovate-lanceolate, 2–4 mm long, symmetric or asymmetric, apices short- to long-acuminate; margins sharply serrate to serrulate above, plane or inflexed on one side below, cells enlarged and bulging, sometimes forming a distinct border; costa none; cells smooth, pellucid, lax, thin-walled, upper and median cells long-hexagonal to linear, 70–180 × 6–20 µm; basal cells enlarged, broadly long-rectangular, extreme basal cells at middle of insertion line often greatly enlarged; alar cells not differentiated. Ventral leaves lanceolate; margins smooth to weakly serrulate, cells not bulging inflated; cells linear, narrow, firm-walled, otherwise similar to dorsal and lateral leaves. Asexual reproduction by gemmae in loose clusters on stems abaxial to the leaf insertions; gemmae green to hyaline, uniseriate, borne terminally on loose filaments. Dioicous. Setae elongate, 15–25 mm long, red to dark red, smooth. Capsules suberect to inclined, cylindric, 1.5–2.5 mm long; exothecial cells rectangular to long-rectangular, lateral walls very thick, horizontal walls thin; stomata on neck, variable in form: perfect, 2-celled and irregularly formed, 2–3-celled; opercula long-rostrate, 1.0–1.5 mm long; annuli well developed, of 5–7 rows of thin-walled, quadrate cells, persistent at the base of the opercula; peristome diplolepideous; exostome teeth narrowly triangular, dorsal (outer) surface red to reddish orange, densely and closely cross-striate below, coarsely papillose above, median furrows narrow, ventral (inner) surface yellowish, lightly papillose; endostome as long as the exostome, yellowish, lightly papillose, basal

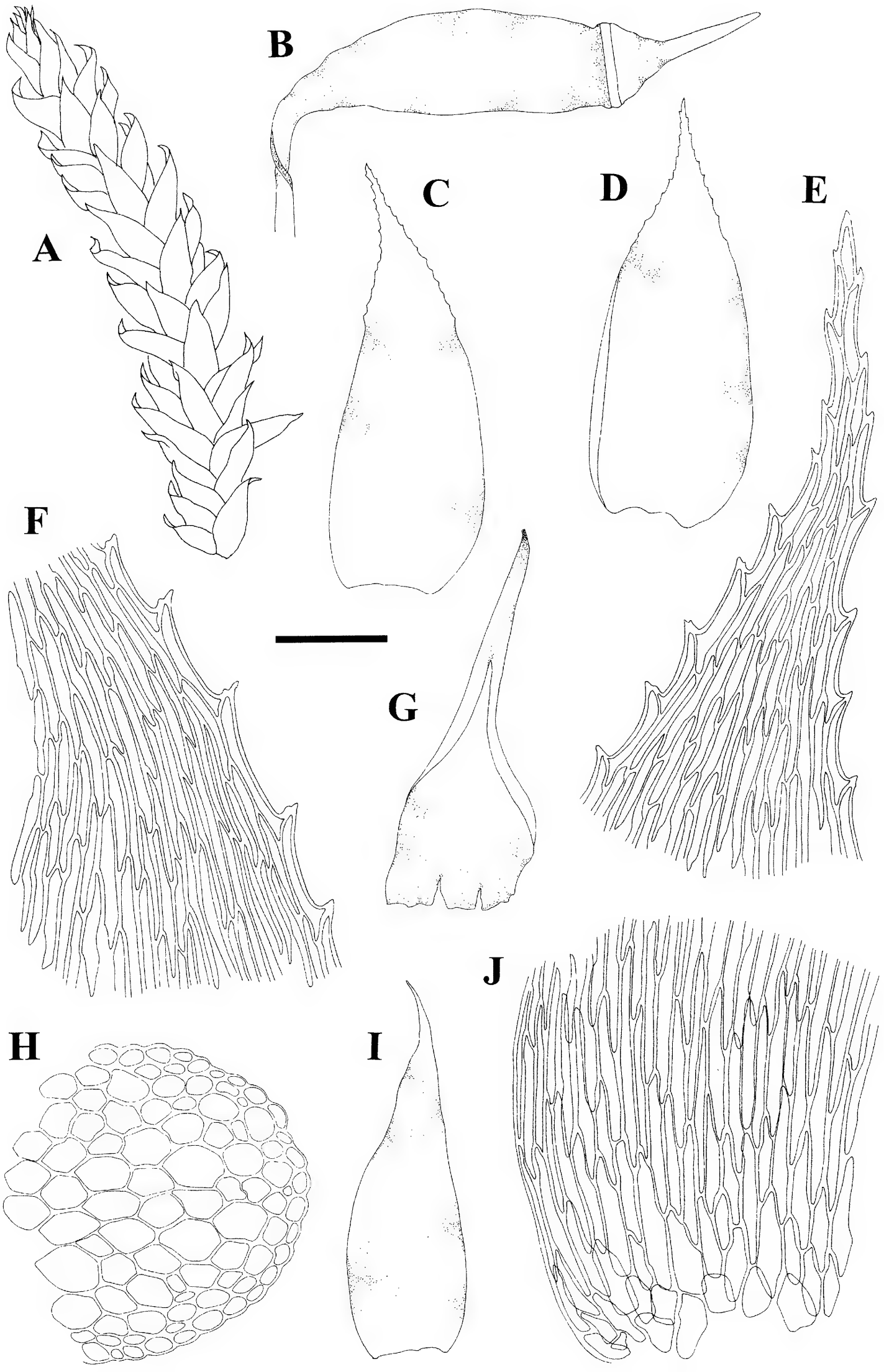


Figure 237. *Rhynchostegiopsis tunguraguana*. A. Habit. B. Seta, capsule, annulus, and operculum. C & D. Lateral leaves. E. Leaf apex. F. Upper leaf cells and margin. G. Calyptra. H. Stem in cross section. I. Ventral leaf. J. Basal and alar cells. Scale in mm: bar = 0.08 (H); bar = 0.09 (E, F, J); bar = 0.6 (C, D, I); bar = 0.9 (B, G); bar = 2.6 (A). All figure parts from *Allen 11067*.

membranes high, segments well developed, keeled, weakly perforate, cilia 1–2, nodose. Spores round, 10–18 µm, smooth to lightly papillose. Calyptrae cucullate, 3 mm long, at times irregularly split at base, naked.

Illustrations. Brotherus (1907a, Fig. 690); Brotherus (1925, Fig. 619); Crum and Bartram (1958, Figs. 23–25); Welch (1971b, Figs. 235–241); Sharp *et al.* (1994, Fig. 630); Churchill and Linares (1995, Fig. 119 c–f); Buck (1998, Pl. 37 8–12); Gradstein *et al.* (2001, Fig. 150 G–K); Price (2001, Fig. 8). Figure 237.

Habitat. On humus, soil, pine or leaf duff, shaded banks, base of trees, palm or treelet trunks, roots, twigs, and rotting logs or stumps, occasionally on rocks, at times pendent; (650–)1800–2850 m.

Distribution in Central America. BELIZE. Toledo: *Allen 18539* (MO, TEFH). GUATEMALA. Baja Verapaz: *Sharp 2766* (FH, US); Quetzaltenango: *Standley 67444* (FH, MO). EL SALVADOR. Chalatenango: *Sipman 37797* (NY). HONDURAS. Comayagua: *Allen 11067* (MO); Francisco Morazán: *Allen 12368* (MO); Lempira: *Allen 11267* (MO); Ocotepeque: *Allen 14481* (MO, TEFH); Olancho: *Allen 12713* (MO). COSTA RICA. Heredia: *Crosby 9860* (CR, MO).

World range: Mexico; Central America; Caribbean; Western and Northern South America, Brazil.

Rhynchostegiopsis tunguraguana is a high elevation, medium-sized species with ovate to ovate-lanceolate, variously acuminate leaves that are laxly complanate when dry. In aspect and color *R. tunguraguana* is similar to *Plagiothecium*, but that genus differs in having decurrent leaves with smooth to lightly serrulate upper margins, non-swollen marginal cells, and short double costae. The stems of *R. tunguraguana* lack internal differentiation. Its leaves have long-hexagonal to linear upper cells; enlarged, broadly rectangular basal cells with the extreme basal cells at middle of the insertion line often greatly enlarged; and undifferentiated alar cells. There are occasional collections of *R. tunguraguana* (*e.g.*, *Allen 18539*, MO) with gemmae that occur in loose clusters on the stems abaxial to the leaf insertions. These gemmae are identical in form to those sometimes seen in *R. flexuosa*, and in both species they occur in the same position as the rhizoids. The gemmae in *R. costaricensis* are different from those of *R. tunguraguana* in that they occur at the base of the dorsal and some lateral leaves on the abaxial side, and they originate from leaf cells as well as stem cells contiguous to the leaf insertions.

In Central America *R. tunguraguana* is distinguished from *R. flexuosa* and *R. carolae* by its medium-sized plants and ovate-lanceolate leaves. *Rhynchostegiopsis flexuosa* often grows at low elevations, and it is a slender species with shorter, lanceolate leaves that are flexuose-contorted when dry. *Rhynchostegiopsis carolae* is a robust species with leaves to 6 mm long. *Rhynchostegiopsis costaricensis* and *R. tunguraguana* are similar in size, and they have identically shaped leaves. The presence of specialized asexual structures that occur at the extreme base of the dorsal and some lateral leaves immediately separates *R. costaricensis* from *R. tunguraguana.* When these structures are absent, the presence in *R. costaricensis* of lateral leaves that are stiffly and smoothly complanate-secund, with the apices pointing straight downward toward the substrate, will distinguish it from *R. tunguraguana*, which has laxly complanate plants with the apices mostly spreading laterally.

HYPOPTERYGIACEAE

Hypopterygiaceae Mitt., J. Proc. Linn. Soc., Bot., Suppl. 1: 147. 1859.

Cyathophoraceae Kindb., Bot. Centralbl. 76: 85. 1898. Hypopterygiaceae trib. Cyathophoreae (Kindb.) M. Fleisch., Musci Buitenzorg 3: 1066. 1908. Hypopterygiaceae subfam. Cyathophoroideae (Kindb.) Broth., Nat. Pflanzenfam. (ed. 2) 11: 276. 1925.

Hypopterygiineae H. A. Mill., Phytologia 21: 251. 1971.

Lophidiaceae Rodway, Pap. & Proc. Roy. Soc. Tasmania 1912: 10. 1912, illegitimate name, includes families with priority.

Plants slender to robust, gregarious or tufted. Primary stems creeping, stolon-like, sympodially branched, secondary stems erect to ascending. Stolons and stems with well-developed central strands (when absent replaced by central cavities), at times with lateral or central cavities, tomentose; rhizoids weakly to strongly pinnately branched, smooth or papillose. Stems simple (*Cyathophorum*) or branched; simple stems not differentiated and mostly horizontal, branched stems differentiated into a vertical or ascending stipe and mostly horizontal, 1–2(–3)-pinnately branched frond. Leaves occasionally 8-ranked, more often 3-ranked, consistently so in distal parts of fronds; 3-ranked branch leaves differentiated into two rows of lateral leaves and a ventral row of amphigastria. Lateral leaves complanate, asymmetric, ovate to oblong-ovate, acute to long-acuminate or hair-pointed; margins entire, serrulate to serrate, or ciliate, usually bordered by linear cells; costae usually single, ending above midleaf to excurrent, at times short and variably single, double, discontinuous, or absent; cells smooth, rounded, rhombic, or oblong-hexagonal, thin- or thick-walled, at times porose; alar cells not differentiated. Amphigastria considerably smaller than lateral leaves, symmetric, erect or appressed. Asexual reproduction by deciduous leaves or by clusters of uniseriate gemmae. Autoicous, synoicous, or dioicous. Perichaetia and perigonia lateral on secondary stems and branches, paraphyses present or absent. Setae short to elongate. Capsules subglobose to oblong-ovoid, erect, inclined or pendent; opercula rostrate; annuli strongly or weakly developed; exothecial cells collenchymatous; stomata phaneroporic, long-pored; peristome diplolepideous, double (single and endostomial in *Catharomnion*); exostome teeth hypnaceous, with closely spaced trabeculae and lamellae cross-striate and papillose on the lower dorsal (outer) surface or daltoniaceous with broadly spaced trabeculae and lamellae evenly papillose throughout; endostome basal membranes high or low, segments keeled (plane to weakly keeled in *Catharomnion*), narrow or broad, perforate or entire, cilia present or absent. Calyptrae cucullate or mitrate, smooth and naked or sparsely hairy.

The Hypopterygiaceae were revised by Kruijer (2002). He placed seven genera in the family: *Dendrohypopterygium* (2 species), *Canalohypopterygium* (1 species), *Catharomnion* (1 species), *Hypopterygium* (7 species), *Lopidium* (2 species), *Dendrocyathophorum* (1 species), and *Cyathophorum* (7 species, including *Cyathophorella*). On the basis of molecular evidence, Stech *et al.* (2002) confirmed the synonymy of *Cyathophorum* and *Cyathophorella* and described a new genus (*Arbusculohypopterygium*) for *Dendrohypopterygium arbuscula*. They did not, however, provide convincing morphological support for *Arbusculohypopterygium*. The family has a mostly Gondwanan distribution, with 11 species known from Indomalaysia, nine from Australasia, five in the New World, and three in Africa. The Hypopterygiaceae are characterized by their creeping stolons and erect to ascending secondary stems that are usually differentiated into a stipe and frond. The family has entirely or partly complanate-foliate stems and branches with 3-ranked leaves that are differentiated into two rows of asymmetric, lateral leaves and a single row of small, symmetric ventral leaves (*i.e.*, amphigastria). Other noteworthy features of the family include: (1) the occasional presence in the stolons, stems, or branches of central or lateral cavities that have oil-like inclusions; (2) typically very well-developed stem central strands; (3) often densely pinnately branched rhizoids that arise from scattered initials; (4) capsules with 2-celled, long-pored stomata; (5) hypnaceous- and daltoniaceous-type peristomes; (6) cucullate and mitrate calyptrae. Cladistical analyses of the Hypopterygiaceae (Kruijer 2002) indicate the family is closely aligned to the Daltoniaceae genera *Achrophyllum* and *Calyptrochaeta.*

1. *Hypopterygium* Brid., Bryol. Univ. 2: 709. 1827.

Plants medium-sized to robust, dark green, green, or yellowish green, gregarious or in dense tufts. Primary stems prostrate, densely radiculose, secondary stems erect or ascending, dendroid to flabellate or palmate, radiculose at base or completely radiculose, hyaline to greenish, becoming red with age; stipes in cross section with weakly differentiated epidermis, firm-walled cortical cells, well-developed central strands; stipes with reduced, well-spaced leaves, frond 1–2(–3)-pinnately branched; paraphyllia absent; pseudoparaphyllia absent, scale leaves present; axillary hairs with short, reddish brown basal cells and elongate, hyaline upper cells; rhizoids from single, scattered initials (at times densely clustered abaxial to the stipe leaf insertions), densely pinnately branched. Leaves in 3 or 8 ranks. Stipes evenly foliate or complanate, leaves monomorphic or dimorphic; frond leaves when 8-ranked not flattened and monomorophic, when 3-ranked flattened and dimorphic with two rows of lateral leaves and a single row of ventral amphigastria. Leaves asymmetric or symmetric; apices acute, broadly or abruptly acuminate; margins entire, serrate or serrate-dentate, usually distinctly and continuously bordered, border occasionally faint and interrupted, or absent; costae usually distinct and single, reaching 1/2–7/8 the leaf length, at times faint or absent in stipe leaves, basal frond leaves, or amphigastria; cells smooth, hexagonal, rectangular, or short-linear; alar cells undifferentiated. Lateral frond leaves asymmetric, broadly ovate to oblong; amphigastria symmetric, broadly ovate, subcircular, obovate, elliptic, or oblong. Asexual reproduction by deciduous leaves or by clusters of uniseriate gemmae on the ultimate branches. Autoicous, synoicous, or dioicous. Setae elongate, red to red brown, smooth throughout or lightly roughened below capsules. Capsules horizontal to pendulous, symmetric, cupulate to ovoid-cylindric, neck well developed; exothecial cells collenchymatous; stomata on neck, 2-celled, long-pored; opercula obliquely long-rostrate; annuli well developed; peristome diplolepideous, exostome median furrow absent, median lines faint, dorsal (outer) surface densely and closely cross-striate and papillose below, coarsely papillose above; endostome lightly papillose, basal membranes high, segments narrow, keeled, usually perforate, cilia 1–3. Calyptrae cucullate (rarely mitrate), 2 mm long, naked, smooth.

Hypopterygium is a genus of seven species (Kruijer 2002) found throughout the tropical, subtropical, and south temperate regions of the world, with outliers in the Pacific Northwest of North America, Hawaii, and the Japan-Korea area. *Hypopterygium* typically is found on tree trunks, rotting wood, and rocks in shaded, wooded places or near streams. Its plants are characteristically dendroid with distinct stipes and 1–2-pinnately branched fronds with complanate leaves. Its stems have a weakly differentiated epidermis and exceptionally well-developed central strands. The outstanding feature of the genus is the presence of strongly dimorphic frond leaves that are usually differentiated into large asymmetric lateral leaves and a single row of small, ventral amphigastria. The lateral leaves vary in shape from broadly ovate to oblong, while the symmetric amphigastria vary from broadly ovate, subcircular, obovate, elliptic, to oblong. The leaf margins are typically distinctly bordered and vary from entire to serrulate to serrate-dentate. The costae are long, single, smooth at back, and usually end above midleaf. The leaves of *Hypopterygium* have a homogeneous areolation in which the cells are smooth and usually hexagonal to rectangular, with undifferentiated alar cells. Asexual reproduction in the genus occurs by means of deciduous leaves or by clusters of uniseriate gemmae on the ultimate branches. *Hypopterygium* has elongate setae that are mostly smooth, but at times the setae are somewhat roughened near the capsules. The capsules of *Hypopterygium* are horizontal to pendent, and they have obliquely long-rostrate opercula, well-developed annuli, and well-formed, 2-celled, long-pored stomata. *Hypopterygium* has a perfect, diplolepideous, hypnaceous peristome. The calyptrae are nearly always cucullate, smooth, and naked.

In Central America *Hypopterygium* cannot be confused with any other moss because of the combination of its dendroid habit and dimorphic frond leaves that are differentiated into two ranks of lateral leaves and a single row of ventral amphigastria. Although the genus is sometimes associated with the Hookeriaceae, a close relationship seems unlikely because of the presence in *Hypopterygium* of: (1) rhizoidal initials scattered on the stems; (2) rhizoids densely pinnately branched; (3) stem central strand exceedingly well developed; (4) lateral leaves/amphigastria differentiation; (5) single costae; (6) cucullate calyptrae; (7) 2-celled, long-pored stomata; (8) hypnaceous peristome. On the other hand, *Hypopterygium* seems more similar to the Daltoniaceae (especially *Achrophyllum*) on the basis

of its rhizoidal characters and single leaf costae. *Achrophyllum* and *Hypopterygium*, in addition, have well-developed stem central strands and similar axillary hairs. Whittemore and Allen (1989) also suggested a close relationship between the Daltoniaceae and Hypopterygiaceae, but their study was compromised by the inclusion of *Cyathophorum* and *Cyathophorella* in the Daltoniaceae. A recent cladistical analysis of the problem (Kruijer 2002) found "strong support for the hypothesis, that the Hypopterygiaceae form a monophyletic group with a group formed by *Achrophyllum* and *Calyptrochaeta* as its sister group."

The name *Hypopterygium* combines the Greek *hypo-* (under) and *pterygion* (a little wing) in reference to its ventral amphigastria.

Hypopterygium tamarisci (Sw.) Brid. *ex* Müll. Hal., Syn. Musc. Frond. 2: 8. 1850. *Hypnum tamarisci* Sw., Fl. Ind. Occid. 3: 1825. 1806. Protologue. Jamaica. *Swartz.*

Hypopterygium rigidulum Mitt., J. Linn. Soc., Bot. 12: 329. 1869. Protologue. [Colombia] Andes Bogotenses, in sylvis prope Bucamaranga et Pacho (6000–7000 ped.) frequens, *Weir, n. 348.*

Hypopterygium pseudotamarisci Müll. Hal., Linnaea 38: 645. 1874. *Hypopterygium tamarisci* subsp. *pseudotamarisci* (C. Müll.) Kindb., Hedwigia 40: 288. 1901. Protologue. Mexico, in sylvis profundis ad arbores muscosas et ligna valde putrida regionis temperatae montosae prope Mirador haud raro, inter 4–5000 pedes altitudinis et in sylvis opacis montosis ad loca humida in ligno putrido vel in terra humosa montis San Cristobal haud frequens, inter 6000–6500 pedes elevationis: *C. Mohr* 1857. Monte Orizaba: *Fréder. Müller*. Xalapa, in lapidibus et arboribus: *v. Chrismar 1849*. Types. Mexico. In sylvis densis ad arborum truncos et truncos prostratos regionis montosa temperata, haud raro sed raro fertile, San Cristobal, Sept. 1857 (US, syntype); Mexico. Hab. In sylvis montosis in terra humosa et ad truncos putridos. Monte San Cristobal, 6000, *C. Mohr N 83* (NY, syntype); Orizaba, Legit. *Fred. Müller* (NY, syntype).

Hypopterygium cubense Müll. Hal. *in* Kindb., Hedwigia 40: 287. 1901, invalid name, in synonymy. Based on: Cuba, rocks in dense woods, *Wright 130.*

Plants medium-sized to somewhat robust, 1–4 cm tall, green to yellowish green, gregarious or in dense tufts. Primary stems prostrate and creeping, densely radiculose, secondary stems erect or ascending, dendroid to flabellate or palmate, frond 1–2-pinnately branched, stipe to 2.5 cm long, radiculose at base or throughout, hyaline to greenish, becoming reddish with age, stipe epidermal cells short-rectangular; stipes in cross section with one row of somewhat enlarged, thin-walled epidermal cells, cortical cells small, firm-walled, central strand massive; paraphyllia absent; pseudoparaphyllia absent, scale leaves present; axillary hairs 2–3 cells long, basal 1–2 cells short-rectangular, reddish brown, upper cell oblong-elongate to elliptical, hyaline; rhizoids from single rectangular initials scattered over the stolons and stipes, at times densely clustered abaxial to the stipe leaf insertions, smooth to lightly roughened, reddish brown, densely pinnately branched. Stipe leaves monomorphic, distantly spaced, clasping at base, recurved to squarrose above, broadly ovate to triangular, to 1.0 mm long, abruptly acuminate, weakly bordered; costae single, ending at or above midleaf. Frond leaves dimorphic: two rows of lateral leaves, single row of ventral amphigastria. Lateral leaves complanate, recurved to slightly contorted when dry, asymmetrical, broadly ovate to oblong-ovate, 0.7–2.0 mm long, gradually to abruptly acuminate; margins entire or serrate above, plane, bordered by 1–3 rows of linear cells; costae single, distinct, ending 1/3–3/4 the leaf length, smooth on back, not projecting at the tips; cells smooth, upper and median cells rhombic to oblong-rhombic, 30–44 × 14–20 µm, firm-walled; basal cells somewhat larger; alar cells undifferentiated. Ventral leaves (amphigastria) erect-appressed, broadly ovate, 0.5–1.0 mm long, acute to subulate; margins entire or serrate, plane, bordered; costae percurrent or excurrent. Asexual reproduction by deciduous leaves or by clusters of uniseriate gemmae on the ultimate branches. Autoicous, synoicous, or dioicous. Setae elongate, 10–20 mm long, red to red brown, smooth throughout or lightly roughened below capsules. Capsules horizontal to pendulous, symmetric, cupulate to ovoid-cylindric, 1–2 mm long, neck well developed, at times pustulate; exothecial cells small, quadrate to oblate in 1–2 rows at the mouth, lower cells rounded to oblong, thin-walled, collenchymatous; stomata on neck, 2-celled, long-pored; opercula long-rostrate, 2.0 mm long; annuli well developed, of 2–4 rows of cells; peristome diplolepideous; exostome teeth yellowish, narrowly triangular, median furrow absent, median lines faint, dorsal (outer) surface densely and closely cross-striate and papillose below, coarsely papillose above, trabeculae extending laterally beyond the lamina, ventral (inner) surface smooth below, papillose above;

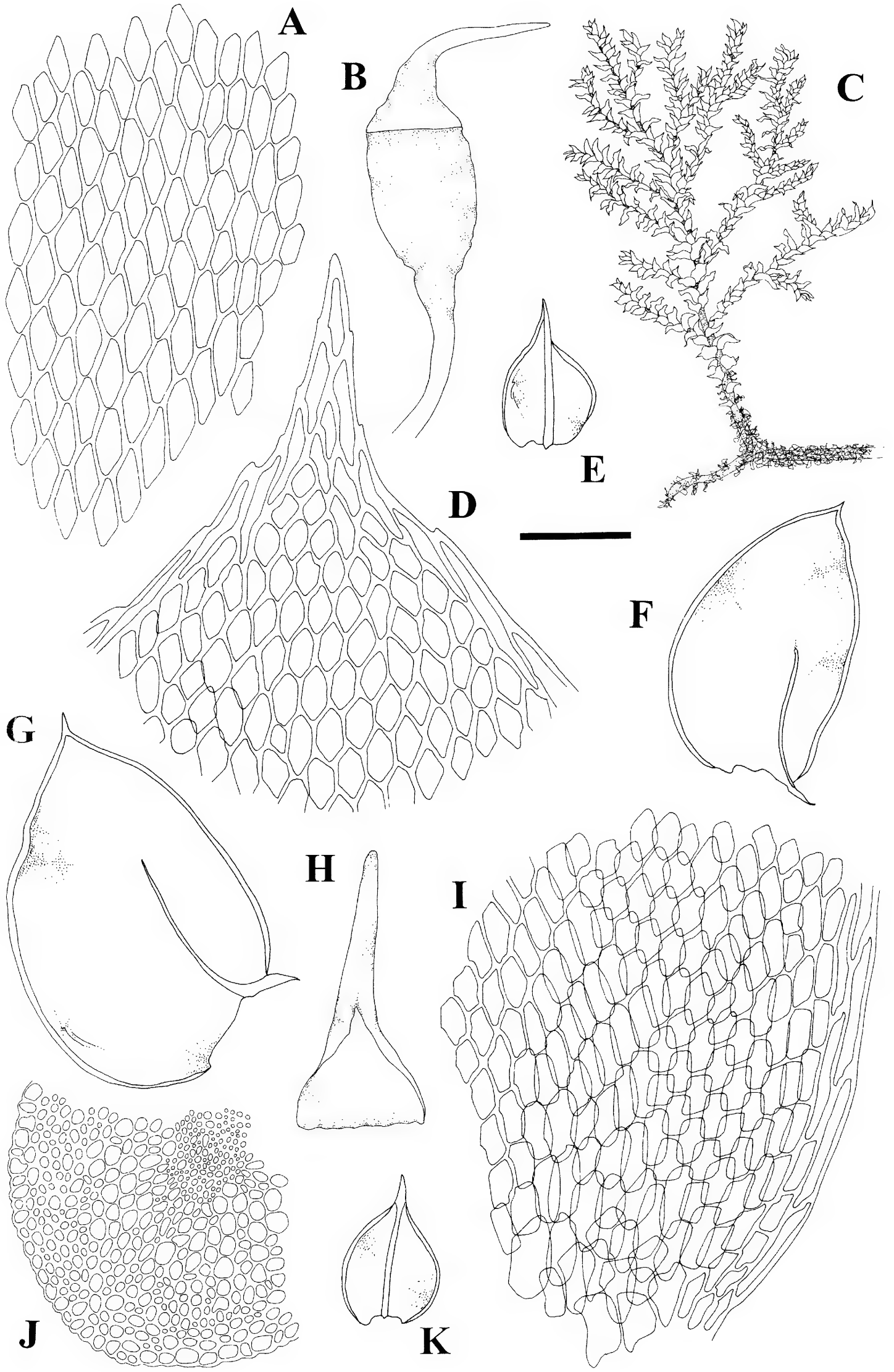
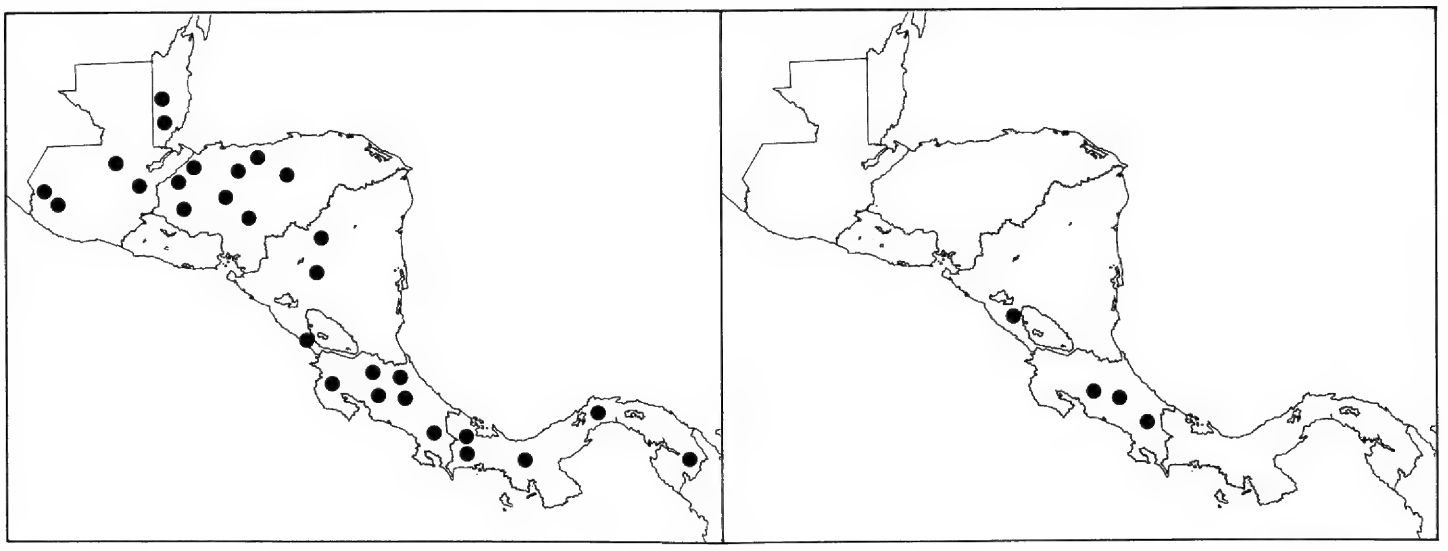


Figure 238. *Hypopterygium tamarisci*. A. Median leaf cells. B. Seta, capsule, and operculum. C. Habit. D. Leaf apex. E & K. Amphigastria. F & G. Lateral leaves. H. Calyptra. I. Basal and alar cells. J. Stem in cross section. Scale in mm: bar = 0.06 (A, D, I); bar = 0.13 (J); bar = 0.7 (E–G, K); bar = 0.8 (B, H); bar = 6.6 (C). B, H from *Allen 15159*; C from *Folsom 4826*; all other figure parts from *Allen 18078*.



Hypopterygium tamarisci *Symphyodon imbricatifolius*

endostome hyaline, faintly roughened below, lightly papillose above, basal membranes high, segments narrow, keeled, perforate, cilia 1–3, nodose. Spores rounded, 10–17 µm, smooth to lightly papillose. Calyptrae cucullate, 2 mm long, naked, smooth.

Illustrations. Hooker (1818, Pl. 35, as *Hypnum larcininum*); Fleischer (1908, Fig. 183, as *Hypopterygium ceylanicum*); Herzog (1926, Fig. 66, as *Hypopterygium monicum*); Bartram (1939, Fig. 355, as *Hypopterygium ceylanicum*); Bartram (1949, Fig. 145 A–D, as *Hypopterygium tamariscinum*); Breen (1963, Pl. 102 1–5, as *Hypopterygium tamariscinum*); Iwatsuki and Sharp (1967, Fig. 3, as *Hypopterygium tenellum*); Whittier (1976, Fig. 80, as *Hypopterygium tahitense*; Fig. 81 A–K, as *Hypopterygium nadeaudianum*; Fig. 81 L–S, as *Hypopterygium arusculosum*); Mohamed and Robinson (1991, Figs. 141–150, as *Hypopterygium tenellum*); Noguchi (1991, Fig. 338, as *Hypopterygium tenellum*); Sharp *et al.* (1994, Fig. 632, as *Hypopterygium tamariscinum*); Churchill and Linares (1995, Fig. 94 d–g, as *Hypopterygium tamariscinum*); So (1995, p. 53, as *Hypopterygium tenellum*); Duarte Bello (1997, Pl. 248, as *Hypopterygium tamariscinum*); Magill and Rooy (1998, Fig. 171 1–13, as *Hypopterygium larcininum*); Gradstein *et al.* (2001, Fig. 143 L–Q); Kruijer (2002, Figs. 29–34). Figure 238.

Habitat. On tree trunks or roots, rotting logs or wood, humus, and rocks (often limestone) or boulders in woods, along or in streams; (180–)500–2500(–3000) m.

Distribution in Central America. BELIZE. Cayo: *Allen 15159* (MO); Toledo: *Allen 18630* (MO). GUATEMALA. Alta Verapaz: *Williams et al. 42101* (F, MO); Quetzaltenango: *Steyermark 33731* (F, FH); San Marcos: *Steyermark 37111* (F, FH); Zacapa: *Steyermark 42615* (F, FH). HONDURAS. Atlántida: *Allen 17612* (MO); Comayagua: *Allen 13767* (MO); Cortés: *Allen 14064* (MO); Francisco Morazán: *Olson 83-10a* (MO); Lempira: *Allen 11329* (MO); Olancho: *Allen 12450* (MO); Santa Bárbara: *Allen 11695* (MO); Yoro: *Liesner 26594* (MO). NICARAGUA. Jinotega: *Henrich & Stevens 293* (HNMN, MO); Matagalpa: *Granzow de la Cerda et al. 2182* (DUKE, MO, NY); Rivas: *Granzow de la Cerda 1686* (DUKE, MO). COSTA RICA. Alajuela: *Liesner 5087* (MO); Cartago: *Maxon & Harvey 8190* (F, FH, US); Guanacaste: *Chávez 138* (CR, MO); Heredia: *Crosby & Crosby 6471* (CR, MO, NY, US); Puntarenas: *Dauphin 1792* (MO); San José: *Skutch 2849* (F, FH, MO, US). PANAMA. Bocas del Toro: *Allen 5301* (MO); Chiriquí: *Allen 5354* (MO); Darién: *Allen 8846* (MO); Panamá: *Crosby 10107* (MO); Veraguas: *Folsom 2945A* (MO, NY, PMA).

World range: Southeastern U.S.A.; Mexico; Central America; Caribbean; Western, Northern, and Southern South America, Brazil; Northeast, West-Central, East, and South Tropical Africa, Southern Africa, Western Indian Ocean; Indian Subcontinent, China, Eastern Asia, Indo-China, Malesia; Australia, New Zealand; Southwestern and South-Central Pacific.

This species is more commonly known in Central America as *Hypopterygium tamariscinum* (Hedw.) Brid. rather than *H. tamarisci* (Sw.) Brid. *ex* Müll. Hal. The confusion surrounding these names occurred when Hedwig listed *Hypnum tamarisci* Sw. (from Jamaica) as a synonym of his new

species and cited type material for *Leskea tamariscina* Hedw. from "Australes et Jamaica." Kruijer (1995) has shown that the description and illustrations of *Leskea tamariscina* refer only to the Australasian type material and that the Jamaican type material is a different taxon. The present name for *Leskea tamariscina* is *Canalohypopterygium tamariscinum* (Hedw.) Kruijer, a narrowly distributed species known only from New Zealand and the Auckland Islands. *Hypopterygium tamarisci* is widely distributed throughout the tropical and south temperate regions of the world.

Hypopterygium tamarisci is a medium-sized species with strongly creeping primary stems and erect or ascending, dendroid to flabellate or palmate secondary stems. It has distinct stipes and 1–2-pinnately branched fronds. Its stems are usually densely radiculose and its rhizoids, which originate from scattered initials, are densely pinnately branched. The fronds of *H. tamarisci* have three ranks of complanate-flattened leaves that are strongly dimorphic: two ranks of large, asymmetric broadly ovate to oblong-ovate lateral leaves and a single rank of small, symmetric amphigastria. The leaves have single costae that end at or a little above midleaf and smooth, rhombic to oblong-rhombic leaf cells. The sporophytes of *H. tamarisci* have elongate setae, long-rostrate opercula, well-developed annuli, collenchymatous exothecial cells, long-pored stomata, and a perfect hypnaceous peristome. Its calyptrae are cucullate.

This beautiful species cannot be confused with any other Central American moss due to the combination of its dendroid to flabellate or palmate plants with well-differentiated stipes, and branches that have 3-ranked, dimorphic leaves in which the ventral leaves form small amphigastria. There are three other Central American genera that have strongly dimorphic leaves with a single row of small amphigastria: *Racopilum*, *Helicophyllum*, and *Rhacopilopsis*. None of these genera, however, has dendroid to flabellate or palmate plants. *Racopilum* further differs in having a dorsal, rather than ventral, row of amphigastria and rhizoids originating from clusters of initials abaxial to the leaf insertions. *Helicophyllum* also differs from *Hypopterygium tamarisci* in having papillose or mammillose leaf cells and immersed, eperistomate capsules that lack stomata and have flat to slightly convex opercula. *Rhacopilopsis* additionally differs from *Hypopterygium* in having leaves with short, double costae, margins often recurved on one side, linear-rhomboidal median cells, and small groups of hyaline, thin-walled, somewhat inflated alar cells. *Hypopterygium tamarisci* has been introduced into Europe, where it grows mostly in greenhouses. It has, however, become established outside in Portugal (Kruijer 2002).

SYMPHYODONTACEAE

Symphyodontaceae M. Fleisch., Musci Buitenzorg 4: 1110. 1923.

Stems prostrate, simple, irregularly pinnately, or tripinnately branched, at times filiform-attenuate; stems in cross section with epidermis of small, thick-walled cells, central strand absent; paraphyllia absent; pseudoparaphyllia absent, scale leaves present; rhizoids from clusters of initials abaxial to the leaf insertions, not or sparsely and irregularly branched. Stem and branch leaves similar or dimorphic, oval, oblong, oblong-ovate, oblong-lanceolate, or lingulate, slightly asymmetric, plane to concave, obtuse, acute, or acuminate, not or shortly decurrent; margins serrulate to serrate, plane or inflexed, often incurved on one side at base; costae short and double; cells usually prorate, firm-walled, median cells linear; alar cells differentiated. Asexual gemmae sometimes present. Dioicous. Setae elongate. Capsules erect to suberect, cylindric to oblong-ovate, symmetric, densely spinose; exothecial cells not collenchymatous; stomata present; opercula conic, apiculate to long-rostrate; annuli well developed; peristome diplolepideous; exostome teeth narrowly triangular, dorsal (outer) surface smooth, faintly papillose, or weakly cross-striate at base, median lines faint; endostome basal membranes low, segments narrow, keeled, perforate, cilia absent. Calyptrae cucullate, naked, smooth.

Fleischer (1923) established the monogeneric Symphyodontaceae and positioned them between the Hookeriaceae and Leucomiaceae. He considered *Symphyodon* closely related to *Chaetomitrium*; their leaves are similarly shaped, with short double costae, typically serrate margins, linear, variably prorate cells, and weakly but clearly differentiated, firm-walled alar cells. The presence in *Symphyodon* of spinose capsules is its most distinctive feature, and this attribute also occurs in *Chaetomitrium*. Although *Symphyodon* has a neckeraceous exostome and that of *Chaetomitrium* is more typically hypnaceous, in both genera the endostomial cilia are absent or rudimentary. The family was synonymized with the Daltoniaceae (Crosby 1974b; Walther 1983; Vitt 1984) based on the erroneous interpretation of its peristome as daltoniaceous. It was subsequently recognized again as a monogeneric family and placed in the Leucodontales suborder Neckerineae (Buck & Vitt 1986; He & Snider 2000), Hookeriales (Buck & Ireland 1994), or Hypnales (Buck 1998). The most recent moss ordinal classifications (Buck & Goffinet 2000; Goffinet & Buck 2004) have dispensed with the Leucodontales and positioned the Symphyodontaceae in the Hypnales. Buck and Goffinet (2000) placed four genera in the Symphyodontaceae (*Chaetomitriopsis*, *Chaetomitrium*, *Dimorphocladon*, and *Symphyodon*) and put the family between the Catagoniaceae and Sematophyllaceae. Goffinet and Buck (2004), as well as Goffinet *et al.* (2009), placed six genera in the family (*Chaetomitriopsis*, *Chaetomitrium*, *Dimorphocladon*, *Symphyodon*, *Trachythecium*, and *Unclejackia*) and put the Symphyodontaceae between the Rhytidiaceae and Plagiotheciaceae.

1. *Symphyodon* Mont., Ann. Sci. Nat., Bot., sér. 2, 16: 279. 1841.

Plants small to large, dull or glossy, golden to yellowish green. Stems prostrate, simple or irregularly pinnately, or tripinnately branched, at times filiform-attenuate, branches sometimes easily detached; stems in cross section with epidermis of small, thick-walled cells, central strand absent; paraphyllia absent; pseudoparaphyllia absent, scale leaves present; rhizoids from small clusters of initials abaxial to the leaf insertions, smooth, not or sparsely and irregularly branched. Stem and branch leaves similar or dimorphic, oval, ovate, oblong, oblong-ovate, oblong-lanceolate, or lingulate, plane to concave, at times undulate, slightly asymmetric, obtuse, acute, or acuminate, not or shortly decurrent; margins serrulate to coarsely serrate, plane or inflexed, often incurved on one side at base; costae short and double, extending to 1/4–1/2 the leaf length; cells smooth or prorate on dorsal surface, firm-walled, median cells linear, extreme apical cells shorter; alar cells more or less differentiated, of several quadrate to short-rectangular cells. Asexual gemmae sometimes present on stems. Dioicous. Setae elongate, smooth below, roughened to papillose above. Capsules erect to suberect, cylindric to oblong-ovate, symmetric, mammillose at the neck, densely spinose above; exothecial cells thick-walled, rectangular, not collenchymatous; stomata present; opercula conic, apiculate to long-rostrate; annuli well developed; peristome diplolepideous; exostome teeth narrowly triangular, dorsal (outer) surface smooth, faintly papillose, or weakly cross-striate at base, median lines faint, ventral (inner)

surface smooth or papillose; endostome basal membranes low, smooth or faintly papillose, segments narrow, keeled, perforate, lightly papillose, cilia absent. Calyptrae cucullate, naked, smooth.

He and Snider (2000), in a revison of *Symphyodon*, recognized 15 species in the genus, only one of which (*S. imbricatifolius*) occurs in the New World. The genus is concentrated in southern and southeastern Asia; there are 12 species in the Indo-Himalayan region. *Symphyodon pygmaeus* (Broth.) He & Snider is the most broadly distributed species; it extends from Mozambique, through Southeast Asia, and into Hawaii. *Symphyodon* has a remarkably homogeneous morphology. It is distinguished gametophytically by its yellowish green plants that lack a stem central strand; stems with scale leaves around its branch primordia; slightly asymmetric, often oblong or lingulate leaves with sharply serrate upper margins; linear, prorate upper leaf cells; and weakly developed, firm-walled alar cells. Sporophytically *Symphyodon* has elongate setae; erect to suberect, symmetric, spinose capsules; well-developed annuli and stomata; and neckeraceous peristomes.

The name *Symphyodon* combines the Greek *sym-* (together) with *phy-* (grow or produce) and *odon* (tooth), in reference to the exostome and endostome, which are sometimes fused at the base.

Symphyodon imbricatifolius (Mitt.) S. P. Churchill, AAU Rep. 35: 194. 1994. *Lepidopilum imbricatifolium* Mitt., J. Linn. Soc., Bot. 12: 372. 1869. Protologue. [Ecuador] Andes Quitenses, in sylva Canelos (3000 ped.), *Spruce, n. 787*. Andes Peruvianae, Tarapoto, in saxis (1500 pd.), *Spruce, n. 786*. Types (see He & Snider 2000). Mont. de Canelos, *Spruce* [*787*] (NY, lectotype); Tarapoto, in saxis, *Spruce* [*786*] (NY) = *Eulacophyllum cultelliforme* (Brid.) W. R. Buck & Ireland.

Taxiphyllum machrisiorum H. A. Crum, Los Angeles County Mus. Contr. Sci. 18: 5. 1957 ["*machrisianum*"]. *Isopterygium machrisiorum* (H. A. Crum) Ireland, Bryologist 87: 356. 1984 [1985]. *Pseudotaxiphyllum machrisiorum* (H. A. Crum) Ireland, Caldasia 16(78): 267. 1991. *Symphyodon machrisiorum* (H. A. Crum) W. R. Buck & Ireland, Bryologist 95: 433. 1992. Protologue. *Dawson 14743a* (holotype, R), *14743b*, along streambed 4 km north of Veadeiros, Chapada dos Veadeiros, Goiás, Brazil, April 30, 1956.

Symphyodon americanus Steere, Brittonia 34: 438. 1982. Protologue. Colombia. Santander: in *Cinchona* forest east of Río Valegra, Cornejo region, Cordillera Oriental, alt. 6000–7000 ft., epiphytic, 15 Nov 1942, *Steere 7534*.

Plants small to medium-sized, glossy, golden to yellowish green, in loose mats, at times pendent. Stems prostrate or ascending, 2–4 cm long, yellowish green when young, distinctly red with age, simple, irregularly or subpinnately branched, at times filiform-attenuate, branches easily detached; stems in cross section with epidermis of 2–3 rows of small, thick-walled cells, cortical cells enlarged, thin-walled, central strand absent; paraphyllia absent; pseudoparaphyllia absent, scale leaves present; axillary hairs 5 cells long, basal 2 cells short-rectangular, reddish brown, upper 3 cells elongate, hyaline; rhizoids from small clusters of initials abaxial to the leaf insertions, smooth, not or sparsely and irregularly branched. Stem leaves appressed to erect or somewhat spreading, closely or somewhat distantly spaced, oblong, oval-oblong, 1.0–1.3 mm long, concave, slightly asymmetric, obtuse to acute, shortly decurrent; margins irregularly serrate above, subentire below, often incurved on one side at base; costae short and double, extending to 1/4 the leaf length; cells smooth or prorate on dorsal surface, firm-walled, median cells linear, 35–70 × 2–4 µm, extreme apical cells shorter; alar cells slightly differentiated, of 4–10 quadrate to short-rectangular cells. Branch leaves ovate to ovate-lanceolate, 0.7–1.0 mm long. Dioicous. Sporophytes not seen; description from Buck and Ireland (1992), Buck (1998), and He and Snider (2000). Setae elongate, to 2 mm long, red, smooth below, roughened above. Capsules erect to suberect, cylindric to oblong-ovate, 1.5–2.6 mm long, symmetric, mammillose at the neck, densely spinose above, spines to 110 µm long; exothecial cells thick-walled, rectangular; stomata present; opercula straight-rostrate, 0.8 mm long; annuli of 2–4 rows of cells; peristome diplolepideous; exostome teeth pale yellow, narrowly triangular at base, filiform above, dorsal (outer) surface smooth to faintly papillose, weakly cross-striate at base; endostome with a low, smooth basal membrane, 50–60 µm high, segments narrow, keeled, perforate, lightly papillose, cilia absent. Spores rounded, 13–18 µm, finely papillose. Calyptra cucullate, naked, smooth.

Illustrations. Crum (1957, Figs. 1–4); Steere (1982, Figs. 20–27); Ireland (1984, Figs. 15–22); Buck and Ireland (1992, Figs. 1–4); Sharp *et al.* (1994, Fig. 572); Churchill and Linares (1995, Fig.

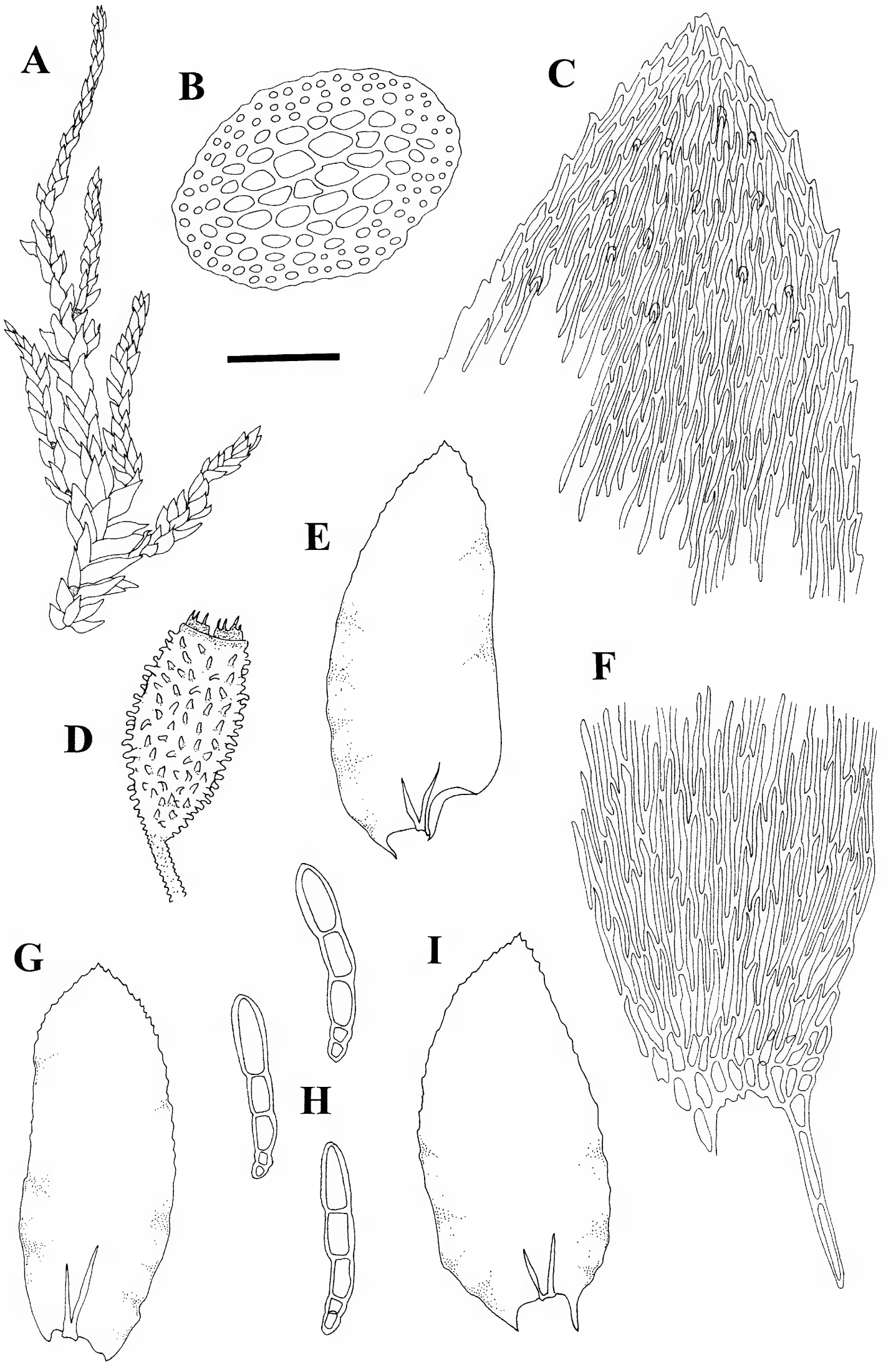


Figure 239. *Symphyodon imbricatifolius*. A. Habit. B. Stem in cross section. C. Leaf apex. D. Seta and capsule. E, G & I. Leaves. F. Basal and alar cells. H. Axillary hairs. Scale in mm: bar = 0.05 (B, C, F, H); bar = 0.16 (E, G, I); bar = 1.0 (D); bar = 1.56 (A). A from *Lyon 230*; D redrawn from He and Snider (2000); all other figure parts from *Crosby & Crosby 6075*.

188 a–e); Buck (1998, Pl. 115); He and Snider (2000, Figs. 92–105); Gradstein *et al.* (2001, Fig. 215 F–K). Figure 239.

Habitat. On small trunks, branches, and shaded rocks; 1000–1800 m.

Distribution in Central America. NICARAGUA. Granada: *Danin 1-G* (MO). COSTA RICA. Cartago: *Crosby & Crosby 6075* (MO); Puntarenas: *Lyon 230* (MO); San José: *Kapelle & Gutiérrez MK1891* (U, vide Buck & Ireland 1992).

World range: Mexico; Central America; Caribbean; Western and Northern South America, Brazil.

Symphyodon imbricatifolius is a small to medium-sized species that often grows as thin mats, with glossy, yellow green, irregularly branched plants and typically erect-appressed leaves. There are only a few collections of *S. imbricatifolius* from Central America, where it is found on tree trunks, branches, or rocks. Its rarity, however, may be due to difficulty in recognizing the species, since capsules are unknown from the region and there is nothing distinctive about its gametophytes to separate it from the Hypnaceae or Sematophyllaceae. Microscopically, the gametophytes exhibit a conspicuous suite of characters that, once known, help in recognizing the species: stem central strand absent; scale leaves around the branch buds; axillary hairs with two short, brown basal cells and three elongate, hyaline upper cells; stem leaves asymmetric, oblong to oblong-oval, bluntly acute, decurrent; upper leaf margins sharply serrate; costa short and double; upper leaf cells linear, often prorate; weakly developed, firm-walled alar cells. Although its sporophytes are unknown in Central America they are, in comparison to all other Central American mosses, unique in having spinose capsules with spines as long as 110 µm.

In Central America the gametophytes of *Symphyodon imbricatifolius* could be mistaken for those of species of *Isopterygium*, *Pseudotaxiphyllum*, *Taxiphyllum*, *Phyllodon*, or *Chryso-hypnum*. All species of *Isopterygium* differ from *S. imbricatifolius* in having filamentous pseudoparaphyllia. The only species of *Pseudotaxiphyllum* in Central America (*P. distichaceum*) differs from *S. imbricatifolius* in having strongly flattened, cultriform leaves and numerous apical, twisted-vermiform asexual propagula. As noted by Buck and Ireland (1992), *S. imbricatifolius* is very similar to *Taxiphyllum laevifolium* (Mitt.) W. R. Buck in leaf shape, marginal toothing, and areolation. *Taxiphyllum laevifolium* differs from *S. imbricatifolius* in having foliose pseudoparaphyllia, non-decurrent leaves, and axillary hairs consisting of a single short, brown basal cell and a single elongate, hyaline cell. *Phyllodon truncatulus* is similar to *S. imbricatifolius* in aspect and leaf shape, but it differs in having a stem central strand, foliose pseudoparaphyllia, leaves with bifid marginal serrations, and leaf cells that are often seriate-papillose as well as prorate. All Central American *Chryso-hypnum* species differ from *S. imbricatifolius* in having foliose pseudoparaphyllia, a weakly developed stem central strand, acuminate leaves, and an autoicous sexual condition.

The name *Taxiphyllum machrisianum* was given in honor of "Mr. and Mrs. Maurice A. Machris" (Crum 1957), and so the correct form of that species name should be *T. machrisiorum* (McNeill 2006).

LITERATURE CITED

Abramov, I. I. & L. A. Volkova. 1998. Handbook of mosses of Karelia. Arctoa 7 (Suppl. 1): 1–390.

Akiyama, H. 1988. Studies on *Leucodon* (Leucodontaceae, Musci) and related genera in East Asia. IV. Taxonomic revision of *Leucodon* in East Asia. J. Hattori Bot. Lab. 65: 1–80.

———. 1994. Suggestions for the delimitation of the Leucodontaceae and the infrageneric classification of the genus *Leucodon*. J. Hattori Bot. Lab. 76: 1–12.

——— & N. Nishimura. 1993. Further studies on branch buds in mosses; "pseudoparaphyllia" and "scaly leaves." J. Pl. Res. 106: 101–108.

———, T. Koponen & D. H. Norris. 1991. Bryophyte flora of the Huon Peninsula, Papua New Guinea. XLV. *Neolindbergia* (Prionodontaceae, Musci). Acta Bot. Fenn. 143: 77–89.

———, H. Tsubota, T. Yamaguchi & M. Suleiman. 2003. The new genus *Benitotania* (Daltoniaceae, Bryopsida) from Mt. Kinabalu. Bryologist 106: 454–459.

Allen, B. H. 1980. Peristome variations in the genus *Fissidens*: an SEM study. Bryologist 83: 314–327.

———. 1981. A reevaluation of the Sorapillaceae. Bryologist 84: 335–338.

———. 1986. The taxonomic status of *Hypnella punctata*. Bryologist 89: 224–226.

———. 1987a. A revision of the Dicnemonaceae (Musci). J. Hattori Bot. Lab. 62: 1–100.

———. 1987b. A revision of the genus *Leucomium* (Leucomiaceae). Mem. New York Bot. Gard. 45: 661–677.

———. 1987c. A revision of the genus *Mesotus* (Musci: Dicranaceae). J. Bryol. 14: 441–452.

———. 1987d. *Hookeriopsis crosbyi* (Musci: Hookeriaceae): a new species from western Panama. Bryologist 90: 45–47.

———. 1987e. Observations on the protonemata of *Drummondia prorepens* (Musci: Orthotrichaceae). Evansia 4: 33–37.

———. 1987f. On distinguishing Pterobryaceae and Meteoriaceae by means of pseudoparaphyllia. Bryol. Times 42: 1–3.

———. 1987g. *Renauldia paradoxica* Allen sp. nov. (Musci, Pterobryaceae). J. Bryol. 14: 677–680.

———. 1990. A revision of the genus *Crossomitrium* (Musci: Hookeriaceae). Trop. Bryol. 2: 3–34.

———. 1994. *Porotrichum tenuinerve* (Musci: Neckeraceae), a new species from Honduras, with a provisional key to *Porotrichum* in Central America. Novon 4: 315–318.

———. 1996. *Diphyscium pocsii* (Musci: Buxbaumiaceae), an African species new to Honduras. Nova Hedwigia 62: 371–375.

———. 1999. A revision of the moss genus *Lepyrodon* (Leucodontales, Lepyrodontaceae). Bryobrothera 5: 23–48.

——— & S. P. Churchill. 2002. A new species of *Thamnobryum* (Musci: Neckeraceae) from Venezuela, with a key to the Neotropical species of *Thamnobryum*. Novon 12: 155–158.

——— & M. R. Crosby. 1986a. A revision of the genera *Pilotrichidium* and *Diploneuron* (Musci: Hookeriaceae). J. Hattori Bot. Lab. 61: 45–64.

——— & ———. 1986b. Revision of the genus *Squamidium* (Musci: Meteoriaceae). J. Hattori Bot. Lab. 61: 423–476.

——— & R. E. Magill. 2003. A revision of *Pilotrichella* (Lembophyllaceae: Musci). Egri Tanárképzö Föisk. Tud. Közlem. 24: 43–83.

——— & ———. 2007. A revision of *Orthostichella* (Neckeraceae). Bryologist 110: 1–45.

———, M. R. Crosby & R. E. Magill. 1986. A review of the genus *Stenodictyon* (Musci). Lindbergia 11: 149–156.

Allison, K. W. & J. Child. 1971. The Mosses of New Zealand. University of Otago Press, Dunedin.

Andrews, A. L. 1952. Taxonomic notes. XI. The case of *Tripterocladium brewerianum*. Bryologist 55: 166–172.

Argent, G. C. G. 1973a. A taxonomic study of African Pterobryaceae and Meteoriaceae. I. Pterobryaceae. J. Bryol. 7: 353–378.

———. 1973b. A taxonomic study of African Pterobryaceae and Meteoriaceae. II. Pterobryaceae—continued. J. Bryol. 7: 563–602.

Arzeni, C. B. 1954. The Pterobryaceae of the southern United States, Mexico, Central America, and the West Indies. Amer. Midl. Naturalist 52: 1–67.

Barthlott, W. & W. Schultze-Motel. 1981. Zur Feinstruktur der Blattoberflächen und systematischen Stellung der Laubmoosgattung *Rhacocarpus* und anderer Hedwigiaceae. Willdenowia 11: 3–11.
Bartram, E. B. 1928a. Costa Rican mosses collected by Paul C. Standley in 1924–1926. Contr. U.S. Natl. Herb. 26: 51–114.
———. 1928b. Mosses of Jamaica. Jamaica Naturalist 1: 15–20.
———. 1929. Additional Costa Rican mosses. J. Wash. Acad. Sci. 19: 11–27.
———. 1931. A review of the American species of *Daltonia*. Bull. Torrey Bot. Club 58: 31–48.
———. 1933a. Manual of Hawaiian mosses. Bernice P. Bishop Mus. Bull. 101: 1–275.
———. 1933b. The Templeton Crocker Expedition of the California Academy of Sciences, 1932. No. 8. Mosses of the Templeton Crocker Expedition collected by John Thomas Howell and lists of the mosses known from the Galapagos Islands and from Cocos Island. Proc. California Acad. Sci. ser. 4, 21: 75–86.
———. 1934. Mosses of southern British Honduras and Guatemala. Rhodora 36: 55–58.
———. 1939. Mosses of the Philippines. Philipp. J. Sci. 68: 1–437.
———. 1946. New species and new combinations of Guatemalan mosses. Bryologist 49: 109–125.
———. 1949. Mosses of Guatemala. Fieldiana, Bot. 25: i–v, 1–442.
———. 1951. Additional Costa Rican mosses. IV. Bryologist 54: 231–242.
Beever, J., K. W. Allison & J. Child. 1992. The Mosses of New Zealand. Second edition. University of Otago Press, Dunedin.
Bescherelle, É. 1872. Prodromus bryologiae mexicanae ou énumération des mousses du Mexique avec description des espèces nouvelles. Mém. Soc. Sci. Nat. Cherbourg 16: 143–256.
———. 1894. Cryptogamae Centrali-Americanae in Guatemala, Costa-Rica, Columbia & Ecuador a cl. F. Lehmann lectae. Bull. Herb. Boissier 2: 389–400.
Bosch, R. B. van den & C. M. van der Sande Lacoste. 1865. Bryologia Javanica. 2 (Fas. 45–46): 105–112. E. J. Brill, Lugduni-Batavorum.
Bowers, F. D. 1994. *Callicostella*. *In*: A. J. Sharp, H. Crum & P. M. Eckel (eds.), The Moss Flora of Mexico. Mem. New York Bot. Gard. 69: 789–792.
Breen, R. S. 1963. Mosses of Florida. An Illustrated Manual. 273 pp. University of Florida Press, Gainesville.
Bridel, S. E. 1827. Bryologia Universa 2: i–ii + 1–732. J. A. Barth, Lipsiae.
Britton, E. G. 1894. Bryophyta. Musci [collected in southwestern Virginia]. Mem. Torrey Bot. Club 4: 172–191.
———. 1906. Notes on nomenclature VI. Bryologist 9: 37–40.
———. 1912. *Leucodontopsis* Cardot (*Leucodoniopsis* R. & C.). Bryologist 15: 26–28.
———. 1913 [1914]. West Indian mosses—1. Bull. Torrey Bot. Club 40: 653–676.
———. 1918. *Jaegerinopsis squarrosa* n. sp. Bryologist 21: 48–50.
——— & R. S. Williams. 1914. Central America mosses. Torreya 14: 24–31.
Brotherus, V. F. 1905a. Cryphaeaceae. *In*: A. Engler & K. Prantl (eds.), Nat. Pflanzenfam. I(3): 736–747.
———. 1905b. Prionodontaceae. *In*: A. Engler & K. Prantl (eds.), Nat. Pflanzenfam. I(3): 763–765.
———. 1906a. Lembophyllaceae. *In*: A. Engler & K. Prantl (eds.), Nat. Pflanzenfam. I(3): 863–864.
———. 1906b. Lepyrodontaceae. *In*: A. Engler & K. Prantl (eds.), Nat. Pflanzenfam. I(3): 771–773.
———. 1906c. Neckeraceae. *In*: A. Engler & K. Prantl (eds.), Nat. Pflanzenfam. I(3): 775–863.
———. 1907a. Hookeriaceae. *In*: A. Engler & K. Prantl (eds.), Nat. Pflanzenfam. I(3): 918–964.
———. 1907b. Lembophyllaceae. *In*: A. Engler & K. Prantl (eds.), Nat. Pflanzenfam. I(3): 865–870.
———. 1907c. Pilotrichaceae. *In*: A. Engler & K. Prantl (eds.), Nat. Pflanzenfam. I(3): 912–916.
———. 1908. Leucomiaceae. *In*: A. Engler & K. Prantl (eds.), Nat. Pflanzenfam. I(3): 1095–1098.
———. 1909. Nachträge und Verbesserungen. *In*: A. Engler & K. Prantl (eds.), Nat. Pflanzenfam. I(3): 1172–1239.
———. 1925. Musci. *In*: A. Engler (ed.), Nat. Pflanzenfam. Second edition. 11: i–iv, 1–542.
———. 1929. Musci. *In*: H. Handel-Mazzetti, Symbolae Sinicae. Botanische Ergebnisse der Expedition der Akademie der Wissenschaften in Wien nach Südwest-China 1914/1918, 4: 1–147.
Brummitt, R. K. 2001. World Geographical Scheme for Recording Plant Distributions. Second edition. [i]–xv + 137 pp. Hunt Institute for Botanical Documentation, Pittsburgh.

Buck, W. R. 1980 [1981]. Animadversions on *Pterigynandrum* with special commentary on *Forsstroemia* and *Leptopterigynandrum.* Bryologist 83: 451–465.
———. 1987. Taxonomic and nomenclatural rearrangement in the Hookeriales with notes on West Indian taxa. Brittonia 39: 210–224.
———. 1988. Another view of familial delimitation in the Hookeriales. J. Hattori Bot. Lab. 64: 29–36.
———. 1989. *Henicodium* replaces *Leucodontopsis* (Pterobryaceae). Bryologist 92: 534.
———. 1990. Contributions to the moss flora of Guyana. Mem. New York Bot. Gard. 64: 184–196.
———. 1991. Notes on Neotropical Pterobryaceae. Brittonia 43: 96–101.
———. 1992. A revision of *Philophyllum* (Hookeriales). Bryologist 95: 334–337.
———. 1994a. A new attempt at understanding the Meteoriaceae. J. Hattori Bot. Lab. 75: 51–72.
———. 1994b. The resurrection of *Orthostichella*. Bryologist 97: 434–435.
———. 1995. The systematic position of the moss genus *Rhacocarpus*. Fragm. Florist. Geobot. 40(1): 127–131.
———. 1998. Pleurocarpous mosses of the West Indies. Mem. New York Bot. Gard. 82: 1–400.
———. 2003. Guide to the plants of central French Guiana. Part 3. Mosses. Mem. New York Bot. Gard. 76(3): i–vi + 1–167.
——— & B. Allen. 1997. Ordinal placement of the Fontinalaceae. Cryptogamie, Bryol. Lichénol. 18: 227–234.
——— & B. Goffinet. 2000. Morphology and classification of mosses, pp. 71–123. *In*: A. J. Shaw & B. Goffinet (eds.), Bryophyte Biology. Cambridge University Press, Cambridge.
——— & D. Griffin III. 1984. *Trachyphyllum*, a moss genus new to South America with notes on African-South American bryogeography. J. Nat. Hist. (London) 18: 63–69.
——— & R. R. Ireland. 1985. A reclassification of the Plagiotheciaceae. Nova Hedwigia 41: 89–125.
——— & ———. 1992. *Symphyodon* (Symphyodontaceae) in the Americas. Bryologist 95: 433–435.
——— & ———. 1994. Symphyodontaceae. *In*: A. J. Sharp, H. Crum & P. M. Eckel (eds.), The Moss Flora of Mexico. Mem. New York Bot. Gard. 69: 767–769.
——— & D. H. Norris. 1996. *Hedwigia stellata* and *H. detonsa* (Hedwigiaceae) in North America. Nova Hedwigia 62: 361–370.
——— & D. H. Vitt. 1986. Suggestions for a new familial classification of pleurocarpous mosses. Taxon 35: 21–60.
———, C. J. Cox, A. J. Shaw & B. Goffinet. 2005. Ordinal relationships of pleurocarpous mosses, with special emphasis on the Hookeriales. Syst. Biodivers. 2: 121–145.
———, B. Goffinet & A. J. Shaw. 2000a. Testing morphological concepts of orders of pleurocarpous mosses (Bryophyta) using phylogenetic reconstructions based on *trnL-trnF* and *rps4* sequences. Molec. Phylogenet. Evol. 16: 180–198.
———, ——— & ———. 2000b. Novel relationships in pleurocarpous mosses as revealed by cpDNA sequences. Bryologist 103: 774–789.
———, A. J. Shaw & C. J. Cox. 2002. A new species of *Leskeodon* (Daltoniaceae) from Ecuador. Brittonia 54: 178–180.
Cardot, J. 1911. Diagnoses préliminaires de mousses mexicaines. Rev. Bryol. 38: 33–43.
Casas, C. 1991. New checklist of Spanish mosses. Orsis 6: 3–26.
Churchill, S. P. 1988. A revision of the moss genus *Lepidopilum* (Callicostaceae). xi + 293 pp. Ph.D. Dissertation, City University of New York.
———. 1994. The mosses of Amazonian Ecuador. AAU Rep. 35: 1–211.
———. 1998. Catalog of Amazonian mosses. J. Hattori Bot. Lab. 85: 191–238.
——— & E. Linares C. 1995. Prodromus Bryologiae Novo-Granatensis. Bibliot. José Jerónimo Triana 12: [i–x] 1–924.
———, D. Griffin III & J. Muñoz. 2000. A checklist of the mosses of the tropical Andean countries. Ruizia 17: 1–230.
Cortini Pedrotii, C. 2001. New checklist of the mosses of Italy. Fl. Medit. 11: 23–107.
Crosby, M. R. 1969a. A revision of the tropical American moss genus *Pilotrichum*. Bryologist 72: 275–343.
———. 1969b. The mosses reported from Panamá. Bryologist 72: 513–521.

———. 1971. A new moss from western Panama—*Squamidium chiriquense*. Ann. Missouri Bot. Gard. 58: 89–91.
———. 1974a. Noteworthy Costa Rican mosses. Brenesia 4: 9–15.
———. 1974b. Toward a revised classification of the Hookeriaceae (Musci). J. Hattori Bot. Lab. 38: 129–141.
———. 1976. *Rhynchostegiopsis carolae* (Musci: Hookeriaceae): A new species from Costa Rica. Ann. Missouri Bot. Gard. 63: 373–375.
——— & B. H. Allen. 1985. *Brymela tutezona* (Musci: Hookeriaceae), a new genus and species from western Panama. Monogr. Syst. Bot. Missouri Bot. Gard. 11: 211–216.
——— & R. E. Magill. 1977. A Dictionary of Mosses. Missouri Botanical Garden, St. Louis.
——— & ———. 1981. A Dictionary of Mosses, 3rd printing. Missouri Botanical Garden, St. Louis.
———, B. H. Allen & R. E. Magill. 1985. A review of the genus *Hypnella*. Bryologist 88: 121–129.
———, R. E. Magill, B. Allen & S. He. 2000. A Checklist of the Mosses. Missouri Botanical Garden, St. Louis.
Crum, H. 1952. Mosses from Honduras. II. Bryologist 55: 279–285.
———. 1957. The Machris Brazilian expedition. Botany: Musci. Los Angeles County Mus. Contr. Sci. 18: 3–8.
———. 1965. Refinements on the Jamaican bryoflora. Trans. Brit. Bryol. Soc. 4: 790–793.
———. 1983. Mosses of the Great Lakes Forest. Third Edition. 417 pp. University Michigan Herbarium, Ann Arbor.
———. 1984. Notes on tropical American mosses. Bryologist 87: 203–216.
———. 1986. Taxonomic and nomenclatural addenda to the Mexican moss flora. Bryologist 89: 23–27.
———. 1991. A partial clarification of the Lembophyllaceae. J. Hattori Bot. Lab. 69: 313–322.
———. 1994a. Hedwigiaceae. *In*: A. J. Sharp, H. Crum & P. M. Eckel (eds.), The Moss Flora of Mexico. Mem. New York Bot. Gard. 69: 662–666.
———. 1994b. *Hemiragis*. *In*: A. J. Sharp, H. Crum & P. M. Eckel (eds.), The Moss Flora of Mexico. Mem. New York Bot. Gard. 69: 825.
———. 1994c. Lepyrodontaceae. *In*: A. J. Sharp, H. Crum & P. M. Eckel (eds.), The Moss Flora of Mexico. Mem. New York Bot. Gard. 69: 703–704.
———. 1994d. Trachypodaceae. *In*: A. J. Sharp, H. Crum & P. M. Eckel (eds.), The Moss Flora of Mexico. Mem. New York Bot. Gard. 69: 701–703.
——— & L. E. Anderson. 1981. Mosses of Eastern North America. Vols. 1 & 2. Columbia University Press, New York.
——— & E. B. Bartram. 1958. A survey of the moss flora of Jamaica. Bull. Inst. Jamaica, Sci. Ser. 8: 1–90.
——— & W. C. Steere. 1957. The mosses of Porto Rico and the Virgin Islands. Sci. Surv. Porto Rico & Virgin Islands 7(4): 395–599.
——— & ———. 1958. A contribution to the bryology of Haiti. Amer. Midl. Naturalist 60: 1–51.
Delgadillo M., C. 1982. Detalles de la morfología foliar de *Rhacocarpus purpurascens* (Hedwigiaceae, Musci). Biotica 7: 401–404.
——— & W. R. Buck. 1988. *Levierella* (Fabroniaceae), a moss genus new to the Americas. Bryologist 91: 53–55.
De Luna, E. 1990. Protonemal development in the Hedwigiaceae (Musci), and its systematic significance. Syst. Bot. 15: 192–204.
———. 1992. Developmental and systematic studies in the Hedwigiaceae. 216 pp. Ph.D. Dissertation, Duke University.
———. 1995. The circumscription and phylogenetic relationships of the Hedwigiaceae (Musci). Syst. Bot. 20: 347–373.
De Sloover, J. L. 1977. Note de bryologie africaine VIII.—*Neckera*, *Neckeropsis*. Bull. Jard. Bot. Belg. 47: 31–48.
———. 1983. Note de bryologie africaine XII.—*Porotrichum* et *Porothamnium*. Bull. Jard. Bot. Belg. 53: 97–152.
Dixon, H. N. 1904. The Student's Handbook of British Mosses. V. T. Sumfield, Eastbourne.
———. 1930. The mosses of Fiji. Proc. Linn. Soc. New South Wales 55: 261–302.

———. 1935. Further contributions to the moss flora of Siam. J. Siam Soc., Nat. Hist. Suppl. 10(1): 1–30.
Dozy, F. & J. M. Molkenboer. 1848. Musci Frondosi Inediti Archipelagi Indici (Fasc. 5–6): 129–185. H. W. Hazenberg & Soc., Lugduni-Batavorum.
——— & ———. 1854. Prodromus Florae Bryologicae Surinamensis. 1–54. Haarlem. [Natuurk. Verh. Holl. Maatsch. Wetensch. Haarlem, ser. 2, 10(3).]
——— & ———. 1863. Bryologia Javanica 2 (Fasc. 36): 49–56. E. J. Brill, Lugduni-Batavorum.
——— & ———. 1865. Bryologia Javanica 2 (Fasc. 45–46): 105–112. E. J. Brill, Lugduni-Batavorum.
——— & ———. 1867. Bryologia Javanica 2 (Fasc. 56–57): 169–176. E. J. Brill, Lugduni-Batavorum.
Duarte Bello, P. P. 1997. Musgos de Cuba. Fontqueria 47: xxii + 717 pp.
Duby, J. E. 1868. Choix de cryptogames exotiques nouvelles ou mal connues. Mém. Soc. Phys. Genève 19: 291–304.
———. 1871. Choix de cryptogames exotiques nouvelles ou peu connues. I. Mousses. Musci Welwitschiani. b. Pleurocarpi et Supplementum. Mém. Soc. Phys. Genève 21: 425–444.
Dusén, P. 1895. New and some little known mosses from the west coast of Africa. I. Kongl. Svenska Vetensk. Acad. Handl. 28: 1–56.
Enroth, J. 1989. Bryophyte flora of the Huon Peninsula, Papua New Guinea. XXVI. Neckeraceae (Musci). Acta. Bot. Fenn. 137: 41–80.
———. 1990. Notes on the Neckeraceae (Musci) 3–7. *Homaliodendron piniforme* comb. nov. and new synonyms in *Porotrichum*, *Himantocladium* and *Neolindbergia*. Nova Hedwigia 51: 551–559.
———. 1991a. A commentary on the moss genus *Bryonorrisia* Stark & Buck (Leskeaceae), with *B. acutifolia* (Mitt.) Enroth *comb. nov.* J. Bryol. 16: 407–412.
———. 1991b. Notes on the Neckeraceae (Musci). 9. *Porotrichum usagarum*, a neglected Tanzanian endemic, with a note on the growth pattern in the Neckeraceae. Ann. Bot. Fenn. 28: 197–200.
———. 1992. Notes on the Neckeraceae (Musci). 13. Taxonomy of the genus *Himantocladium.* Ann. Bot. Fenn. 29: 79–88.
———. 1993. Notes on the Neckeraceae (Musci). 17. A taxonomic study on the genus *Neckeropsis* in Africa. J. Hattori Bot. Lab. 73: 159–173.
———. 1994a. A taxonomic monograph of the genus *Pinnatella* (Neckeraceae, Bryopsida). Acta Bot. Fenn. 151: 1–90.
———. 1994b. On the evolution and circumscription of the Neckeraceae (Musci). J. Hattori Bot. Lab. 76: 13–20.
———. 1995. Notes on the Neckeraceae (Musci). 21–22. A taxonomic study of *Porotrichopsis flacca* and *Neckeropsis inundata*. Fragm. Flor. Geobot. 40: 181–188.
——— & N. G. Hodgetts. 1996. British Bryological Society expedition to Mulanje Mountain, Malawi. 5. Neckeraceae (Musci). J. Bryol. 19: 135–141.
——— & R. E. Magill. 1994. *Neckeropsis pocsii* (Neckeraceae, Musci), a new species from the Comoro Islands. Bryologist 97: 171–173.
Fleischer, M. 1905a. Neue Gattungen und Arten, herausgegeben in Exs. Musci Archipelagi Indici Serie VII (1904). Hedwigia 44: 301–329.
———. 1905b. Neue Familien, Gattungen und Arten der Laubmoose. I. Teil. Hedwigia 45: 53–64.
———. 1906. Neue Familien, Gattungen und Arten der Laubmoose. I. Teil. Hedwigia 45: 65–87.
———. 1908. Die Musci der Flora von Buitenzorg. Volume 3: i–xxiv, 645–1103. E. J. Brill, Leiden.
———. 1914. Kritische revision von Carl Müllerschen Laubmoosgattungen. Hedwigia 55: 280–285.
———. 1923. Die Musci der Flora von Buitenzorg. Volume 4: i–xxxi, 1105–1729. E. J. Brill, Leiden.
Florschütz, P. A. 1954. Notes on American Musci. Acta Bot. Neerl. 3: 94–99.
———. 1964. Musci. *In*: J. Lanjouw (ed.), Flora of Suriname 6(1): 1–271. E. J. Brill, Leiden.
Florschütz-de Waard, J. 1986. Musci (Part II). *In*: A. L. Stoffers & J. C. Lindeman (eds.), Flora of Suriname. 6(1): i–x + 273–361. E. J. Brill, Leiden.
———. 1990. A catalogue of the bryophytes of the Guianas. II. Musci. Trop. Bryol. 3: 89–104.
Frahm, J.-P. 1982. Grossdisjunktion von Arealen sudamerikanischer und afrikanischer *Campylopus*. Lindbergia 8: 45–52.
———. 1996. Revision der Gattung *Rhacocarpus* Lindb. (Musci). Cryptog. Bryol. Lichénol. 17: 39–65.
——— & J. Eggers. 2001. Lexikon Deutschsprachiger Bryologen. 672 pp. Books on Demand, Norderstedt, Germany.

———, I. Capesium & H. Geiger. 1997. Zur systematischen Position von *Rhacocarpus* Lindb. (Musci, Rhacocarpaceae). Nova Hedwigia 64: 231–241.
Gangulee, H. C. 1976. Mosses of Eastern India and Adjacent Areas. Fasc. 5: 1135–1462. S. N. Guha Ray, Calcutta.
———. 1977. Mosses of Eastern India and Adjacent Areas. Fasc. 6: 1463–1546. S. N. Guha Ray, Calcutta.
Goffinet, B. & W. R. Buck. 2004. Systematics of Bryophyta (mosses): From molecules to a revised classification. Monogr. Syst. Bot. Missouri Bot. Gard. 98: 205–239.
———, ——— & A. J. Shaw. 2009. Morphology, anatomy, and classification of the Bryophyta, pp. 55–138. *In*: B. Goffinet & A. J. Shaw (eds.), Bryophyte Biology. Second edition. Cambridge University Press, Cambridge.
Gradstein, S. R., S. P. Churchill & N. Salazar-Allen. 2001. Guide to the bryophytes of tropical America. Mem. New York Bot. Gard. 86: i–viii, 1–577.
Granzow-de la Cerda, Í. 1997. Revision and phylogenetic study of *Anomodon* and *Herpetineuron* (Anomodontaceae, Musci). Contr. Univ. Michigan Herb. 21: 205–275.
Griffin, 1970. Notes on the tropical genus *Prionodon* (Musci). Rev. Bryol. Lichénol. 653–656.
———. 1973. *Prionodon luteo-virens* (Tayl.) Mitt. and *P. dichotomus* Hampe. Taxon 22: 257–258.
———. 1994. Prionodontaceae. *In*: A. J. Sharp, H. Crum & P. M. Eckel (eds.), The Moss Flora of Mexico. Mem. New York Bot. Gard. 69: 696–701.
Grout, A. J. 1910. Mosses with a Hand-Lens and Microscope. Part 5: [319]–416. Published by the author, New York City.
———. 1934. Moss Flora of North America North of Mexico 3(4): 179–277. Published by the author, Newfane Vermont.
Hampe, E. 1844. Icones Muscorum Novorum vel Minus Cognitorum. Three decades. Henry & Cohen, Bonn.
———. 1862a. Beitrag zu einer Moosflora von Neu-Granada. Flora 45: 449–458.
———. 1862b. Species novas Muscorum ab Dr. Alexandro Lindigio in Nova-Granada mensibus Julio et Augusto a. 1861 collectas, proposuit E. Hampe. Linnaea 31: 518–532.
———. 1865. Prodromus Florae Novo-Granatensis: Musci. Ann. Sci. Nat., Bot. sér. 5, 4: 324–378.
He, S. 1997. A revision of *Homalia* (Musci: Neckeraceae). J. Hattori Bot. Lab. 81: 1–52.
——— & J. A. Snider. 2000. A taxonomic revision of *Symphyodon* (Musci: Symphyodontaceae). Bryologist 103: 52–81.
Hedenäs, L. 1994. The *Hedwigia ciliata* complex in Sweden, with notes on the occurrence of the taxa in Fennoscandia. J. Bryol. 18: 139–157.
———. 1998. Hedwigiaceae, pp. 368–372. *In*: E. Nyholm, Illustrated Flora of Nordic Mosses. Fasc. 4. Aulacomniaceae–Meesiaceae–Catoscopiaceae–Bartramiaceae–Timmiaceae–Encalyptaceae–Grimmiaceae–Ptychomitriaceae–Hedwigiaceae–Orthotrichaceae. Nordic Bryological Society, Copenhagen & Lund.
Hedwig, J. 1801. Species Muscorum Frondosorum. 350 pp. J. A. Barth, Leipzig.
Herzog, T. 1916. Die Bryophyten meiner zweiten Reise durch Bolivia. Biblioth. Bot. 87: 1–347.
———. 1926. Geographie der Moose. XI + 439 + 8 pls. Gustav Fischer, Jena.
———. 1942. Beiträge zur Kenntnis neotropischer Bryophyten. Beih. Bot. Centralbl., Abt. 2, 61: 559–590.
Hooker, W. J. 1808. Musci Nepalenses; or descriptions of several new mosses from Nepal. Trans. Linn. Soc. London 9: 307–322.
———. 1816. Plantae cryptogamicae, quas in plaga orbis novi aequinoctali collegerunt Alexander de Humboldt et Amat. Bonpland. [8] pp. & 4 pls. Veneunt apud J. Harding, London.
———. 1818. Musci Exotici. Vol. 1. Pls. 1–96. Longman, Hurst, Rees, Orme, and Brown, London.
——— & R. K. Greville. 1825. On the genus *Hookeria* of Smith, of the order Musci. Edinburgh J. Sci. 2(2): 221–236.
——— & T. Taylor. 1818. Muscologia Britannica. 140 pp. Longman, Hurst, Rees, Orme, and Brown, London.
Hornschuch, F. 1820. Musci frondosi exotici herbarii Willdenowiani tum Capensis a. b. Bergio lecti tum alii quidam ex Australasiae aliisque orbis terraquei plagis a. l. de Chamissone relati, pp.

[55]–68. *In*: C. G. Nees ab Esenbeck, Horae Physicae Berolinenses. Collectae ex symbolis Virorum Doctorum.

———. 1840. Musci. *In*: C. F. P. von Martius, Flora Brasiliensis 1(2): 1–100. R. Oldenbourg, Monachii et Lipsiae [Munich & Leipzig].

Huttunen, S., M. S. Ignatov, K. Müller & D. Quandt. 2004. Phylogeny and evolution of epiphytism in the three moss families Meteoriaceae, Brachytheciaceae, and Lembophyllaceae. Monogr. Syst. Bot. Missouri Bot. Gard. 98: 328–361.

Hyvönen, J. 1989. Bryophyte flora of the Huon Peninsula, Papua New Guinea. XXVI. Pterobryaceae (Musci). Acta Bot. Fenn. 137: 1–40.

Ignatov, M. S. & E. A. Ignatova. 2003. Moss Flora of the Middle European Russia. Vol. 2: Fontinalaceae–Amblystegiaceae. Arctoa 11(suppl. 2): 612–960.

Ireland, R. R. 1982. Moss Flora of the Maritime Provinces. Publ. Bot. (Ottawa) 13: 1–738.

———. 1984 [1985]. Studies on Mexican mosses. Bryologist 87: 355–360.

Iwatsuki, Z. 1963. A revision of the East Asiatic species of the genus *Anomodon*. J. Hattori Bot. Lab. 26: 27–62.

——— & A. J. Sharp. 1967. Mosses of Yakushima Island, southern Japan. J. Hattori Bot. Lab. 30: 277–314.

Jennings, O. E. 1951. A manual of mosses of western Pennsylvania and adjacent regions. Second edition. Amer. Midl. Naturalist, Monogr. 6: 1–396.

Jones, G. N. 1933. Grimmiaceae. *In*: A. J. Grout (ed.), Moss Flora of North America North of Mexico 2(1): 1–65. Published by the author, Newfane, Vermont.

Kindberg, N. C. 1897. European and N. American Bryineae (Mosses). Part 1: [1]–152. Linköpings Lithografiska Aktiebolag, Sweden.

———. 1899. Studien über die Systematik der pleurokarpischen Laubmosse. II. Bot. Centralbl. 77: 49–55.

Koponen, T. & D. H. Norris. 1986. Bryophyte flora of the Huon Peninsula, Papua New Guinea. XVII. Grimmiaceae, Racopilaceae and Hedwigiaceae (Musci). Acta Bot. Fenn. 133: 81–106.

Kruijer, H. 1995 [1996]. *Canalohypopterygium tamariscinum* (Hedw.) Kruijer: Typification and synonymy of a new combination. Lindbergia 20: 85–88.

———. 2002. Hypopterygiaceae of the World. Blumea (Suppl) 13: [iv] + 1–388.

Lai, M.-J. & T. Koponen. 1981. A synopsis of the genus *Taiwanobryum* (Musci, Prionodontaceae) with notes on *Neolindbergia brassii*. Ann. Bot. Fenn. 18: 117–122.

Lawton, E. 1971. Moss Flora of the Pacific Northwest. xiii + 362 pp., 195 pl. Hattori Botanical Laboratory, Nichinan.

Lewis, M. 1992. *Meteoridium* and *Zelometeorium* in Bolivia. Trop. Bryol. 5: 35–53.

——— & B. Allen. 1992. *Hypnella ambrosia* (Bryopsida: Hookeriaceae), a new species from Bolivia. Novon 2: 355–357.

Li, Xing-jiang (ed.). 1985. Bryoflora of Xizang [Tibet]. x + 581 pp. Science Press, Beijing.

Lin, P.-J. & B. C. Tan. 1995. Contribution to the bryoflora of China (12): A taxonomic revision of Chinese Hookeriaceae (Musci). Harvard Pap. Bot. 7: 25–68.

Lin, S.-L. 1983. A taxonomic revision of Phyllogoniaceae (Bryopsida). Part 1. J. Taiwan Mus. 36(2): 37–86.

———. 1984. A taxonomic revision of Phyllogoniaceae (Bryopsida). Part II. J. Taiwan Mus. 37(2): 1–54.

Lindberg, S. O. 1862 [1863]. Om ett nytt slägte, *Epipterygium*, bland bladmossorna. Oefvers. Förh. Kongl. Svenska Vetensk.-Akad. 19(10): 599–609.

Magill, R. E. 1981. Flora of Southern Africa. Bryophyta. Part 1. Mosses. Fascicle 1. Sphagnaceae–Grimmiaceae. i–xv + 291 pp. Government Printer, Pretoria.

———. 1983. On the circumscription of Pterobryaceae. Beih. Nova Hedwigia 71: 273–279.

———. 1994. Pterobryaceae. *In*: A. J. Sharp, H. Crum & P. M. Eckel (eds.), The Moss Flora of Mexico. Mem. New York Bot. Gard. 69: 705–718.

——— & B. Allen. 1992. *Portorichum cavifolium* comb. nov. (Musci: Neckeraceae). Novon 2: 123.

——— & J. van Rooy. 1998. Flora of Southern Africa. Bryophyta. Part 1. Musci. Fascicle 3. Erpodiaceae–Hookeriaceae. i–vii + 445–622 pp. Government Printer, Pretoria.

Manuel, M. G. 1973a. Studies in Cryphaeaceae I. A revision of the genus *Cryphaea* in North America North of Mexico. Bryologist 76: 144–162.
———. 1973b. Studies in Cryphaeaceae II. A review of the monospecific genus *Dendropogonella* Britt. Bryologist 76: 521–527.
———. 1974. A revised classification of the Leucodontaceae and a revision of the subfamily Alsioideae. Bryologist 77: 531–550.
———. 1977a. A monograph of the genus *Zelometeorium* Manuel, *gen. nov.* (Bryopsida: Meteoriaceae). J. Hattori Bot. Lab. 43: 107–126.
———. 1977b. Studies in Cryphaeaceae III. *Sphaerotheciella* Fleisch. new to the Americas. Occas. Pap. Farlow Herb. Cryptog. Bot 12: 35–40.
———. 1977c. The genus *Meteoridium* (C. Müll.) Manuel, stat. nov. (Bryopsida: Meteoriaceae). Lindbergia 4: 45–55.
———. 1981. Studies in Cryphaeaceae V. A revision of the family in Mexico, Central America and the Caribbean. J. Hattori. Bot. Lab. 49: 115–140.
———. 1982. A brief review of the systematics of the Leucodontaceae and the Cryphaeaceae. Beih. Nova Hedwigia 71: 281–289.
Margadant, W. D. 1968. Early bryological literature. A descriptive bibliography of selected publications treating Musci during the first decades of the nineteenth century and especially in the years 1825, 1826 and 1827. xi + VIII + 277 pp. Thesis. Utrecht.
——— & H. During. 1982. Beknopte Flora van Nederlandse Blad- en Levermossen. W. J. Thieme, Zutphen.
——— & P. Geissler. 1995. Seventeen proposals concerning nomina conservanda for genera of Musci. Taxon 44: 613–624.
McNeill, J., F. R. Barrie, H. M. Burdet, V. Demoulin, D. L. Hawksworth, K. Marhold, D. H. Nicolson, J. Prado, P. C. Silva, J. E. Skog, J. H. Wiersema & N. J. Turland. 2006. International Code of Botanical Nomenclature (Vienna Code). Regnum Veg. 146: [i]–xviii, 1–568.
Menzel, M. 1991. A taxonomic review of the genera *Lindigia* Hampe (Meteoriaceae, Leucodontales) and *Aerolindigia* gen. nov. (Brachytheciaceae, Hypnales), Bryopsida. Nova Hedwigia 52: 319–335.
———. 1992. The bryophytes of Sabah (North Borneo) with special reference to the BRYOTROP transect of Mount Kinabalu. XVII. Meteoriaceae (Leucodontales, Bryopsida). Willdenowia 22: 171–196.
——— & W. Schultze-Motel. 1994. Taxonomische Notizen zur Gattung *Trachycladiella* (Fleisch.) stat. nov. (Meteoriaceae, Leucodontales). J. Hattori Bot. Lab. 75: 73–83.
Michaux, A. 1803. Flora Boreali-Americana, sistens caracteres plantarum quas in America Septentrionali collegit et detexit Andreas Michaux. Vol. 1: 1–329; Vol. 2: 1–340. Levrault, Paris.
Miller, H. A. 1971. An overview of the Hookeriales. Phytologia 21: 243–252.
Mitten, W. 1859. Musci Indiae Orientalis: An Enumeration of the Mosses of the East Indies. J. Proc. Linn. Soc., Bot., Suppl. 2: 1–171.
———. 1869. Musci Austro-Americani. J. Linn. Soc., Bot. 12: 1–659.
———. 1875. Muscineae, pp. 357–374. *In*: J. C. Melliss, St. Helena. London.
Mohamed, H. & H. Robinson. 1991. A taxonomic revision of the moss families Hookeriaceae and Hypopterygiaceae in Malaya. Smithsonian Contr. Bot. 80: i–iv + 1–44.
Mönkemeyer, W. 1927. Die Laubmoose Europas. IV. Andreales–Bryales. 960 pp. E. Haberland, Leipzig.
Müller, C. 1850. Synopsis Muscorum Frondosorum 2(1): 1–160. A. Foerstner, Berlin.
———. 1875. Musci Schweinfurthiani in itineribus duobus in Africam Centralen per annos 1868–1871 collecti, determinati et expositi. Linnaea 39: 325–374.
———. 1874. Novitates Bryothecae Müllerianae. Linnaea 38: 545–620.
———. 1896. Bryologia Hawaiica adjectis nonnullis muscis novis oceanicis. Flora 82: 434–479.
Nebel, M. & G. Philippi. 2001. Die Moose Baden-Württembergs. Bd. 2: Spezieller Teil (Bryophytina II, Schistostegales bis Hypnobryales). 529 pp. Stuttgart (Hohenheim), Ulmer GmbH & Co.
Newton, A. E. 1993. Phylogenetic systematics of the tropical moss genus *Pireella* (Pterobryaceae: Musci). ix + 255 pp. Ph.D. dissertation, Duke University.
———. 2002. Flagelliform propagules from alar cells in *Pilotrichella flexilis*. J. Bryol. 24: 252–254.
Ninh, T. 1984. A revision of Indochinese *Homaliodendron.* J. Hattori Bot. Lab. 57: 1–39.

Noguchi, A. 1936. Contributions to the moss flora of Formosa 5. Trans. Nat. Hist. Soc. Taiwan 26: 139–147.
———. 1957. A revision of the genus *Haplohymenium* Doz. et Molk. (Musci). Kumamoto J. Sci., Sect. 2, Biol. 3: 20–31.
———. 1971. Miscellaneous notes on mosses (2). Misc. Bryol. Lichenol. 5: 139–140.
———. 1976. A taxonomic account of the family Meteoriaceae in Asia. J. Hattori Bot. Lab. 41: 231–257.
———. 1989. Illustrated Moss Flora of Japan. Part 3: 493–742 + vi. Hattori Botanical Laboratory, Nichinan.
———. 1991. Illustrated Moss Flora of Japan. Part 4: 743–1012. Hattori Botanical Laboratory, Nichinan.
Norris, D. H. & T. Koponen. 1985. Bryophyte flora of the Huon Peninsula, Papua New Guinea. VII. Trachypodaceae, Thuidiaceae and Meteoriaceae (Musci). Acta Bot. Fenn. 131: 1–51.
Nyholm, E. 1960. Illustrated Moss Flora of Fennoscandia. II. Musci. Fasc. 4: 287–408. Natural Science Research Council, Stockholm.
Ochyra, R. & J. Enroth. 1989. *Neckeropsis touwii* (Musci, Neckeraceae), new species from Papua New Guinea, with an evaluation of sect. *Pseudoparaphysanthus* of *Neckeropsis*. Ann. Bot. Fenn. 26: 127–132.
———, H. Bednarek-Ochyra, T. Pócs & M. R. Crosby. 1992. The moss *Adelothecium bogotense* in continental Africa, with a review of its world range. Bryologist 95: 287–295.
Palisot de Beauvois, A. M. F. J. 1805. Prodrome des Cinquième et Sixième Familles de l'Aethéogamie. 114 pp. De L'Imprimerie de Fournier Fils, Paris.
Parra Cuspoca, J. D., J. A. Posada García & R. Callejas Posa. 1999. Guía Ilustrada de los Briofitos del Parque ARVÍ (Piedras Blancas). 162 pp. Universidad de Antioquia, Colombia.
Pedersen, N. & L. Hedenäs. 2001. Phylogenetic relationships within the Plagiotheciaceae. Lindbergia 26: 62–76.
——— & ———. 2002. Phylogeny of the Plagiotheciaceae based on molecular and morphological evidence. Bryologist 105: 310–324.
Potier de la Varde, M. R. 1925. Mousses nouvelles de l'Afrique tropicale française. (Diagnoses préliminaires 3e note). Bull. Soc. Bot. France 72: 351–367.
———. 1928. Mousses de l'Oubangui. Arch. Bot. Mém. 1(3): 1–153.
———. 1936. Mousses du Gabon. Mém. Soc. Sci. Nat. Cherbourg sér. 5, 42: 1–270.
———. 1950. Espèces et variétés nouvelles récoltées à Madagascar par M. le Professeur H. Humbert au cours de son 6e et de son 7e voyage. Rev. Bryol. Lichénol. 19: 145–154.
Price, M. 2001. Revision of *Rhynchostegiopsis* (Leucomiaceae: Musci). Ann. Missouri Bot. Gard. 88: 694–712.
Pursell, R. A. 2007. Fissidentaceae. Fl. Neotrop. Monogr. 101: 1–279.
Quandt, D. & S. Huttunen. 2004. Evolution of pendent life-forms in bryophytes. J. Hattori Bot. Lab. 95: 207–217.
Rao, P. 2001. Monographic studies on *Cryphaea* (Bryopsida). Bryobrothera 7: 1–112.
Reese, W. D. 1984. Mosses of the Gulf South. 252 pp. Louisiana State University Press, Baton Rouge.
———. 1985. Tropical lowland mosses disjunct between Africa and the Americas, including *Calyptothecium planifrons* (Ren. & Par.) Argent, new to the Western Hemisphere. Acta Amazonica, Supl. 15: 115–121.
——— & S. Orbán. 1986. *Syrrhopodon incompletus* var. *incompletus* (Musci: Calymperaceae) disjunct between the Americas and Africa. Bryologist 89: 213–214.
Reinwardt, [C. G. C.] & [C. F.] Hornschuch. 1829. Musci Frondosi Javanici. Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 14(2): 697–732.
Renauld, F. 1909. Supplément au Prodrome de la Flore Bryologique de Madagascar. 139 pp. Monaco.
——— & J. Cardot. 1899. Mousses (Atlas): pls. 65–106. *In*: A. & G. Grandidier, Histoire physique, naturelle et politique de Madagascar. 39: 1–562.
Restrepo Restrepo, J. D. & J. D. Para Cuspoca. 2000. Hongos y Musgos del Valle de Aburrá. 153 pp. J. G. R. Arango (ed.). Área Metropolitana del Valle de Aburrá, Colombia.
Richards, P. W. 1934. XLI—Musci collected by the Oxford Expedition to British Guiana in 1929. Bull. Misc. Inform. Kew 8: 317–337.

Robinson, H. 1967. Preliminary studies on the bryophytes of Colombia. Bryologist 70: 1–61.
———. 1971a. A new species of *Cyclodictyon* from Costa Rica. Phytologia 21: 4–5.
———. 1971b. Scanning electron microscope studies on moss leaves and peristomes. Bryologist 74: 473–483.
———. 1972. The status of the genus *Cryphidium* (Bryophyta: Musci). Phytologia 23: 149–150.
———. 1975. The mosses of the Juan Fernandez Islands. Smithsonian Contr. Bot. 27: i–iv + 1–88.
———. 1986. On the relationships of the Hookeriaceae. Bryol. Times 35: 2–3.
——— & D. Griffin III. 1975. A new species of *Rhynchostegiopsis* from Costa Rica. Phytologia 30: 281–283.
Rykovsky, G. F. & O. M. Maslovsky. 2004. Flora of Belarus. Bryophytes. Vol. 1 Andreaeaopsida–Bryopsida. 437 pp. Minsk.
Sainsbury, G. O. K. 1955. A handbook of the New Zealand mosses. Bull. Roy. Soc. New Zealand 5: 1–490.
Sastre-De Jesús, I. 1987. A Revision of the Neckeraceae Schimp. and the Thamnobryaceae Marg. & Dur. in the Neotropics. Ph.D. Dissertation, City University of New York.
———, S. P. Churchill & M. Escobar. 1986. Catálogo de musgos del Departamento de Antioquia, Colombia. Actual. Biol. 15: 77–94.
Sayre, G. 1975. Cryptogamae exsiccatae—an annotated bibliography of exsiccatae of Algae, Lichenes, Hepaticae, and Musci. V. Unpublished exsiccatae. I. Collectors. Mem. New York Bot. Gard. 19: 277–423.
Schimper, W. P. 1843. *Dendropogon* (Baumbart), eine Gattung der Laubmoose. Bot. Zeitung (Berlin) 1: 377–381.
Schwägrichen, F. 1816. Species Muscorum Frondosorum Supplementum 1(2): 1–373, Tab. 50–100. J. A. Barth, Lipsiae.
———. 1826. Species Muscorum Frondosorum Supplementum 2(2)1: 1–79, Tab. 151–175. J. A. Barth, Lipsiae.
———. 1828. Species Muscorum Frondosorum Supplementum 3(1)2: Tab. 226–250. J. A. Barth, Lipsiae.
Scott, G. A. M. & I. G. Stone. 1976. The Mosses of Southern Australia. 495 pp. Academic Press, London.
Sharp, A. J, H. Crum & P. M. Eckel (eds.). 1994. The Moss Flora of Mexico. Mem. New York Bot. Gard. 69: i–x, 1–1113, I–XVII.
Smith, A. J. E. 1978. The Moss Flora of Britain and Ireland. 706 pp. Cambridge University Press, Cambridge.
———. 2004. The Moss Flora of Britain and Ireland. Second edition. 1012 pp. Cambridge University Press, Cambridge.
Smith, D. K. 1994. Neckeraceae. *In*: A. J. Sharp, H. Crum & P. M. Eckel (eds.), The Moss Flora of Mexico. Mem. New York Bot. Gard. 69: 741–765.
Smith, J. E. 1808. Characters of *Hookeria*, a new genus of mosses, with descriptions of ten species. Trans. Linn. Soc. 9: 272–282.
So, M. L. 1995. Mosses and Liverworts of Hong Kong. xi + 162 pp. Heavenly People Depot, Hong Kong.
Spessard, L. L. 1980. A monograph of the genus *Meteorium* (= *Papillaria* Jaeg., *pro parte*) of Mexico. vii + 167 pp. Ph.D. dissertation, University of Tennessee, Knoxville.
Spessard-Schueth, L. 1994a. *Aerobryopsis*. *In*: A. J. Sharp, H. Crum & P. M. Eckel (eds.), The Moss Flora of Mexico. Mem. New York Bot. Gard. 69: 725–726.
———. 1994b. *Pilotrichella*. *In*: A. J. Sharp, H. Crum & P. M. Eckel (eds.), The Moss Flora of Mexico. Mem. New York Bot. Gard. 69: 719–721.
Stafleu, F. A. & R. S. Cowan. 1979. Taxonomic Literature. Volume II: H–Le. Regnum Veg. 98: i–xviii, 1–991.
——— & ———. 1981. Taxonomic Literature. Volume III: Lh–O. Regnum Veg. 105: xii + 1–980.
——— & ———. 1983. Taxonomic Literature. Volume IV: P–Sak. Regnum Veg. 110: 1–1214.
Stech, M., T. Pfeiffer & W. Frey. 2002. Molecular generic classification of the Hypopterygiaceae (Bryopsida), with the description of a new genus, *Arbusculohypopterygium* gen. nov. Studies in austral temperate rain forest bryophytes 10. New Zealand J. Bot. 40: 207–221.

Steere, W. C. 1982. Four new species of Musci from the Andes of Ecuador and Colombia. Brittonia 34: 435–441.

Streimann, H. 1991. Taxonomic studies on Australian Meteoriaceae (Musci). 2: The genera *Aerobryopsis*, *Barbella*, *Floribundaria*, *Meteoriopsis*, *Meteorium* and *Weymouthia*. J. Hattori Bot. Lab. 69: 277–312.

———. 1993. *Barbella trichophora*, an older name for *B. cubensis* (Musci: Meteoriaceae). Bryologist 96: 223–225.

Sullivant, W. S. 1859 [1860]. United States Exploring Expedition. During the years 1838, 1839, 1840, 1841, 1842. Under the command of Charles Wilkes, U.S.N. Botany. Musci. [5]–112. C. Sherman & Son, Philadelphia.

———. 1864. Icones Muscorum or figures and descriptions of most of the mosses peculiar to eastern North America which have not been heretofore figured. viii + 216 pp., pls. 1–128. Sever & Francis, Cambridge, Massachusetts.

Tan, B. C. & H. Mohamed. 1990. Novelties for Peninsular Malayan moss flora. Cryptog. Bryol. Lichénol. 11: 353–362.

——— & H. Robinson. 1990. A review of the Philippine Hookeriaceous taxa (Musci). Smithsonian Contr. Bot. 75: i–iv, 1–41.

Tangney, R. S. 1997. A generic revision of the Lembophyllaceae. J. Hattori Bot. Lab. 81: 123–153.

Thériot, I. 1910. Biographical sketch of Monsieur Renauld. Bryologist 13: 113–116.

———. 1921. Mousses du Costa Rica. Recueil Publ. Soc. Havraise Études Diverses 88: 307–315.

———. 1925. Notes bryologiques. Bull. Soc. Bot. Genève 17: 252–257.

———. 1926. Mexican mosses collected by Brother Arsène Brouard. Smithsonian Misc. Collect. 78(2): 1–29.

———. 1940. Complément au catalogue des Mousses de Cuba III. Mem. Soc. Cub. Hist. Nat. "Felipe Poey" 14(4): 349–372.

Touw, A. 1962. Revision of the moss-genus *Neckeropsis* (Neckeraceae) I. Asiatic and Pacific species. Blumea 11: 373–425.

———. 1972. Additional notes on *Neckeropsis*. Lindbergia 1: 184–188.

——— & R. Ochyra. 1987. Additional notes on *Neckeropsis* 2. Lindbergia 13: 97–104.

Vaz, T. de F. & D. P. da Costa. 2006a. Os gêneros *Brymela*, *Callicostella*, *Crossomitrium*, *Cyclodictyon*, *Hookeriopsis*, *Hypnella* e *Trachyxiphium* (Pilotrichaceae, Bryophyta) no Estado do Rio de Janeiro, Brasil. Acta Bot. Brasil. 20: 955–973.

——— & ———. 2006b. Os gêneros *Lepidopilidium*, *Lepidopilum*, *Pilotrichum* e *Thamniopsis* (Pilotrichaceae, Bryophyta) no Estado do Rio de Janeiro, Brasil. Acta Bot. Brasil. 20: 975–993.

Veling, K. 1996. Leucomiaceae, pp. 365–370. *In*: A. R. A. Görts-Van Rijn (ed.), Flora of the Guianas, Series C, Bryophytes (Musci III). Royal Botanic Gardens, Kew.

Visnadi, S. R. & B. Allen. 1991. A revision of the genus *Lindigia* (Musci: Meteoriaceae) in the Neotropics. Bryologist 94: 5–15.

Vitt, D. H. 1984. Classification of the Bryopsida. *In*: R. M. Schuster (ed.), New Manual of Bryology 2(13): 696–759. Hattori Botanical Laboratory, Nichinan.

Wagner, K. A. 1951. The Neckeraceae of North America. 195 pp. Ph.D. Dissertation, University of Michigan.

———. 1952. Notes on the Neckeraceae. I. New names and new species. Bryologist 55: 143–147.

Walther, K. 1983. Syllabus der Pflanzenfamilien. Vol. 2. Bryophytina, Laubmoose. 108 pp. G. Borntraeger, Berlin.

Welch, W. H. 1962. The Hookeriaceae of the United States and Canada. Bryologist 65: 1–24.

———. 1966. The Hookeriaceae of Mexico. Bryologist 69: 1–68.

———. 1969. The Hookeriaceae of Cuba. Bryologist 72: 93–136.

———. 1971a. *Lepidopilum subtortifolium* Bartr. in North America: Mexico. Bryologist 74: 212–213.

———. 1971b. The Hookeriaceae of Jamaica, Hispaniola, and Puerto Rico. Bryologist 74: 77–130.

———. 1972a [1973]. The Hookeriaceae of the Lesser Antilles. Bryologist 75: 404–455.

———. 1972b [1973]. Hookeriaceae: North America and West Indies, additions and appendix. Bryologist 75: 456–461.

———. 1974. The Hookeriaceae of Central America. Bryologist 77: 328–404.

Whittemore, A. & B. Allen. 1989. The systematic position of *Adelothecium* Mitt., and the familial classification of the Hookeriales (Musci). Bryologist 92: 261–272.

Whittier, H. O. 1976. Mosses of the Society Islands. x + 410 pp. University Presses of Florida, Gainesville.

Wijk, R. van der. 1957. Distichous and pseudodistichous mosses. Acta Bot. Neerl. 6: 386–391.

———, W. D. Margadant & P. A. Florschütz. 1964. Index Muscorum. Vol. III (*Hypnum*–O). Regnum Veg. 33: 1–529.

Williams, R. S. 1924. Galapagos and Cocos Island mosses collected by Alban Stewart in 1905–6. Bryologist 27: 37–45.

———. 1925. Some undescribed mosses from Colombia. Bryologist 28: 59–64.

———. 1927. Mosses of Peru collected by the Captain Marshall Field Peruvian Expedition, 1923. Field Mus. Nat. Hist., Bot. Ser. 4(5): 125–139.

Willis, B. 1939. Mosses of Barro Colorado Island, Canal Zone. Bryologist 42: 152–158.

Wilson, W. 1846. Remarks on the new species of Musci from Quito and Swan River, indicated by Dr. Taylor in the London Journal of Botany, Vol. V. p. 41. London J. Bot. 5: 447–455.

———. 1854. Musci, pp. 244–245. *In*: B. Seemann, The Botany of the Voyage of H.M.S. Herald, under the command of Captain Henry Kellett, R.N., C.B., during the years 1845–51. Part 4. Flora of the Isthmus of Panama. London.

Winkler, S. 1965. Beiträge zur Bryologie von El Salvador, C. A.—I. Laubmoose. Rev. Bryol. Lichénol. 35: 303–369.

Wu, Peng-cheng & Mei-zhi Wang (eds.). 2000. Bryoflora of Hengduan Mts. (Southwest China). xvii + 742 pp. Science Press, Beijing.

Yano, O. 1996. Criptógamos do Parque Estadual das Fontes do Ipiranga, São Paulo, SP. Briófitas, 1: Mniaceae, Rhizogoniaceae, Racopilaceae, Phyllogoniaceae e Leucobryaceae (Bryales). Hoehnea 23(2): 81–98.

Zanten, B. O. van. 1959. Trachypodaceae, a critical revision. Blumea 9: 477–575.

INDEX

Names and page numbers in *italics* indicate synonyms; names in **bold** indicate nomenclatural novelties; page numbers in **bold** indicate descriptions of taxa; page numbers with an asterisk (*) indicate an illustration; page numbers with an exclamation mark (!) indicate a map.

Achrophyllum, 522, 693
Acosta
  cuspidata, *679*
  strumosa, *677*
Acrocryphaea, *57*
  coffeae, *58*
  concavifolia, *58*
  gardneri, *58*
  julacea, *61*
    var. *costaricensis, 58*
  mexicana, 58
  rubricaulis, 63
Acrophyllum, 392
Actinodontium, **434**
  integrifolium, 436
  portoricense, 438
  pygmaeum, **436**, 437*, 438!
  sprucei, **436**, 438!, 439*, 575
  standleyi, 438
Adelotheciaceae, 386
Adelothecium, **387**
  bogotense, **388**, 389*, 390!
Aerobryopsis, 151
  longissima, 168
  martinicensis, 168
Aerolindigia, **101**
  capillacea, **102**, 103*, 104!
Amblytropis, **440**, 514
  denticulata, *511*
  gemmacea, 441
  hispidula, **441**, 442*, 443!
  ovata, 441
  pocsii, *511*
  setosa, 441, 444
Anictangium
  humboldtii, *35*
  imberbe, *28*
Anoectangium
  secundum, *20*
Anomodontaceae, **1**
Anomodon, **2**
  sect. *Haplohymenium*, *10*
  sect. *Herpetineuron*, *12*
  subgen. Pseudoanomodon, 9
  attenuatus, **3**, 4*, 5!
  dentatus, 2
  flexilis, *121*
  integerrimus, 7
  minor, 7
    var. inaequalifolius, **5**!, 6*
  planatus, 7
  rostratus, **7**, 8*, 9!
  thraustus, 7, 10, 12
  toccoae, *13*
  trichophyllum, *170*
  tristis, *10*
  wrightii, *3*
Antitrichia
  cuspidata, *121*
Aptychella
  proligera, 119
Arbuscula, *354*
Arbusculohypopterygium, 693
Astrodontium
  curvirostris, *81*

Barbella, 105
  sect. *Dicladiella*, *105*
  cubensis, *107*
  diclados, *107*
  enervis, *107*
  tenuissima, *119*
  trichophora, *107*
  trichophoroides, *107*
Barbellopsis, **105**
  macroblasta, 105
  trichophora, 104!, **105**, 106*, 136
Braunia, **17**, 127
  andrieuxii, 15!, **17**, 18*
  liebmanniana, *22*, 24
  plicata, 24
  secunda, 19!, **20**, 21*
    var. *andrieuxii*, *17*
    var. *crassiretis*, *20*
  sphaerocarpa, *22*
  squarrulosa, 19!, **22**, 23*
Brymela, **444**
  angustiretis, 443!, **445**, 446*
  callicostelloides, *464*
  complanata, **447**, 448*, 449!
  crosbyi, **449**!, 450*
  cuspidata, 453
  laevinervis, **451**, 452*, 453!
  obtusifolia, 453!, **454**, 455*
  parkiana, 458
  rugulosa, 466
  tutezona, **454**, 456*, 457!
  websteri, 457!, **458**, 459*
Bryobrothera, 386
Bryonorrisia, *12*

Bryowijkia, 66
Bryoxiphium, 252

Callicostaceae, *363*
Callicosta, *364*
andersonii, *365*
bipinnata, *370*
delicatula, *381*
evanescens, *375*
Callicostella, **460**
aquatica, *472*
bernoullii, **462**, 463*, 464!
callicostelloides, **464**!, 465*
ciliata, *469*
colombica, *625*
cruceana, *472*
depressa, 472, 478
filescens, *651*
grossiretis, *625*
hondurensis, *467*
incurva, *641*
lorifolia, *601*
merkelii, **467**, 468*, 469!
mexicana, *467*
oerstediana, **469**!, 470*
pallida, **472**, 473*, 474!
rivularis, *651*
rufescens, 474!, **475**, 476*
subfissidentoides, *651*
subpallida, *472*
tenerrima, *625*
tuberculosa, *472*
vatteri, *467*
Calyptothecium, **183**, 198, 242
sect. *Pseudo-Pterobryopsis*, *183*
sect. *Pseudo-Calyptothecium*, *183*
sect. *Pseudo-Neckera*, *183*
acutifolium, *184*, 186
duplicatum, 180!, **184**, 185*, 325
planifrons, **187**!, 188*
porodictyon, *184*
turgescens, *184*, 186
Calyptrochaeta, **391**, 693
haitensis, 390!, **392**, 393*, 394*
Camptochaete, 169
Campylopus, 387
Canalohypopterygium, 693
tamariscinum, 698
Catagoniaceae, **262**
Catagonium, **262**
sect. *Eucatagonium*, *262*
brevicaudatum, **263**, 264*, 265!
Catharomnion, 693
Chaetephora, *391*
subgen. *Eriopus*, *391*
Chaetomitriopsis, 699
Chaetomitrium, 699
Chaetophora
incurva, *641*
pendula, *646*
Chryso-hypnum, 702
Clastobryum
trichophyllum, *170*
Climaciella
subfrondosa, *243*
Climacium
subgen. *Porotrichum*, *325*
longirostre, *339*
Crossomitrium, 451, **478**, 522
acuminatum, **480**, 481*, 482!
calomicron, *482*
cruegeri, *486*
cubense, *482*
epiphyllum, **482!**, 483*
filiferum, *588*
herminieri, *486*
heterodontium, *486*
jamaicense, *486*
oerstedianum, *482*
orbiculatum, *482*
patrisiae, **484**, 485*, 486!
portoricense, *546*
radulaeforme, *486*
ramulicola, *486*
rotundifolium, 486!, **488**, 489*, 581
saprophilum, **490**, 491*, 492!
scabrisetum, **492**!, 493*
sintenisii, *486*
splendens, *488*
splitgerberi, *486*
spruceanum, *486*
subepiphyllum, *486*
Cryphaceaceae, 31, **38**
Cryphaea, **39**, 127, 211
sect. *Acrocryphaea*, *57*
sect. *Dendropogon*, *54*
apiculata, **41**, 42*, 43!
apiculata, *63*
attenuata, **43**!, 44*
coffeae, *58*
concavifolia, *58*
filiformis, **45**, 46*, 47!
gardneri, *58*
gracillima, *66*
intermedia, *52*
jamesonii, **47**!, 48*
julacea, *61*
leptoclada, *75*
macrospora, 66
mittenii, *63*
nitidula, *47*
orizabae, **49**, 50*, 51!

pachycarpa, *68*
patens, 51!, **52**, 53*
pinnata, *70*
polycarpa, *52*
reticulata, *47*
rubricaulis, *63*
rufescens, *54*
sartorii, *52*
tenuissima, *117*
Cryphaeophilum, 38
Cryphidium
ovalifolia, 40
Cryphidium, *39*
Cryptopapillaria, 154
penicillata, 127, 157, 168
Cryptopodia, *281*
Cryptotheca
cochlearifolia, *246*
densa, *239*
mexicana, *243*
Cyathophoraceae, *693*
Cyathophorella, 522, 693
Cyathophorum, 522, 693
Cyclodictyon, 426, **494**
albicans, **496**, 497*, 498!
albicaule, *499*
arsenei, 513
bernoullii, *462*
bicolor, 498!, **499**, 500*
brittoniae, *565*
capillatum, *506*
crosbyi, **501**, 502*, 503!
cuspidatum, *504*
densifolium, *499*
dussii, *499*
erubescens, *509*
fendleri, 503!, **504**, 505*
humectatum, *499*
jamesonii, *441*
limbatulum, *499*
lindigianum, *496*
lindigianum var. *acunae*, *504*
maxoni, *646*
obliquicuspis, *506*
prasiophyllum, *499*
richardsii, 503
roridum, **506**, 507*, 508!
rubrisetum, 508!, **509**, 510*
subtortifolium, **511**, 512*, 513!, 598
ulophyllum, *499*
validirugosum, 513!, **514**, 515*
varians, **514**, 516*, 517!
Cylindrothecium
amplirete, *555*
Cyptodon, 38, 54
Cyptodontopsis, 38, 54
Daltoniaceae, **386**
Daltonia, **395**
sect. *Pilotrichum*, *364*
aristifolia, *411*
bipinnata, *370*
brevicuspidata, *404*
brevinervis, 399
crispata, *404*
disticha, *293*
dussii, *404*
fenestrellata, 399
filiformis, *45*
gomezii, **397**, 398*, 399!
gracilis, **399**!, 400*
irrorata, *402*
latolimbata, 399
lindigiana, **402**, 403*, 404!
longifolia, **404**!, 405*
lorifolia, *413*
peruviana, **406**, 407*, 408!
polytrichoides, *583*
pulvinata, 408!, **409**, 410*
robusta, *404*
scabriseta, *586*
splachnoides, 401
stenophylla, **411**, 412*, 413!
stewartii, *402*
tenuifola, **413**!, 414*
trachydontia, *415*
trachyodonta, **415**, 416*, 417!
undulata, *298*
Dendroalsia, 38
Dendrocryphaea, 38, 54
Dendrocyathophorum, 522, 693
Dendrohypopterygium, 693
Dendropogon, *54*
rufescens, *54*
Dendropogonella, **54**
rufescens, **54**, 56*, 57!
Dicladiella, *105*
cubensis, *107*
trichophora, *107*
Dicnemonaceae, 31, 66
Dimorphocladon, 699
Diphyscium, 387
Dissodon
mariei, *427*
Distichia
retusa, *293*
undulata, *298*
Distichophyllaceae, *386*
Distichophyllidium, 386
Distichophyllum, 418
sect. *Adelothecium*, *387*
andicola, *419*
auratum, *422*

Distichophyllum *(continued)*
cubense, *424*
elongatum, *424*
geheebii, *388*
longipilum, *424*
mariei, *427*
palmarum, *427*
pusillum, *422*
Dolichomitra, 316
Drummondia, 24, 66
Dusenia
pycnothallodes, *236*
Duthiella, 151

Ectropothecium, 682
Eleutera, *281*
disticha, *293*
Eleuteria, *281*
Entodon
ampliretis, *555*
Eriodon
brevisetus, *112*
longipes, *324*
Eriopus, *391*
haitensis, *392*
Eucatagonium, *262*
brevicaudatum, *263*
Eupilotrichum, *364*
fasciculatum, *378*
filigranum, *381*

Fallaciella, 169
Felipponea, *78*
Fifea, 169
Fissidens, 252
dominicensis, *184*
Floribundaria, **108**
sect. *Eufloribundaria*, *108*
sect. Trachycladiella, 108
flaccida, **109**, 110*, 111!, 125, 168
floribunda, 109
tenuisima, *117*
Fontinalis, 32, 91
disticha, *293*
Forsstroemiaceae, **74**
Forsstroemia, 75
japonica, 75

Garovaglia
mexicana, *243*
planifrons, *187*
scariosa, *195*
ulei, *197*
Glossadelphus, 526

Grimmia
julacea, *61*
julacea, 63
Gymnostomum
imberbe, *28*

Haplohymenium, 1, **10**
triste, 9!, **10**, 11*
Harpophyllum
aureum, *519*
Harrisonia, *31*
apiculata, *33*
humboldtii, *35*
secunda, *20*
squarrulosa, *22*
Hedwigiaceae, **16**, 31
Hedwigia, **24**
albicans fo. *subrevoluta*, *25*
ciliata, 24, 27, 30
var. leucophaea, 24, 27
detonsa, 24
filiformis, 30
humboldtii, *35*
imberbis, *28*
integrifolia, 30
liebmanniana, *22*
nivalis, **25**, 26*, 27!
secunda, *20*
squarrulosa, *22*
stellata, 24, 27
subrevoluta, *25*
Hedwigidium, **27**
imberbe, 27!, **28**, 29*
squarrulosum, *22*
Helicophyllum, 698
Hemiragis, **518**
aurea, 458, 517!, **519**, 520*
friedrichsthaliana, *519*
striata, *519*
Henicodium, 75, **189**
cameruniae, 189
geniculatum, 187!, **190**, 191*
var. gracilis, 192
var. latifolia, 192
niam-niamiae, *190*
siamensis, 189
Herpetineuron, 1, **12**
acutifolium, 2, 13, 15
toccoae, 1, **13**, 14*, 15!
Herzogiella, 262
Hildebrantiella, 198, 246, 250
guyanensis, *199*
pentagona, *199*
tetragona, *208*

Himantocladium, 293
Homaliaceae, *266*
Homalia, **267**
sect. *Isodrepanium*, *277*
angustifrons, *278*
defoliata, *268*
flabellata, *272*
glabella, 265!, **268**, 269*, 280, 581
lentula, *278*
membranacea, *278*
mohriana, *272*
mohrii, *272*
scalpellifolia, *272*
Homaliodendron, **271**
decompositum, *272*
exiguum, 271
flabellatum, **272**, 273*, 274!
mohrianum, *272*
piniforme, 274!, **275**, 276*, 315, 327
punctulatum, 271
scalpellifolium, *272*
Hookeriaceae, **432**
subfam. *Hookeriopsidoideae*, *432*
Hookeria, **521**
sect. *Amblytropis*, *440*
sect. *Callicostella*, *460*
sect. *Eriopus*, *391*
sect. *Hemiragis*, *518*
sect. *Hypnella*, *525*
sect. *Lepidopilidium*, *541*
sect. *Lepidopilum*, *549*
sect. *Scleroneuron*, *364*
sect. *Stenodesmus*, *609*
sect. *Stenodictyon*, *612*
subgen. *Callicostella*, *460*
subgen. *Chaetephora*, *391*
subgen. *Hypnella*, *525*
subgen. *Lophobryum*, *391*
subsect. *Euhypnella*, *525*
subsect. *Hylotapis*, *525*
subsect. *Thamniopsis*, *623*
acicularis, *658*
acutifolia, **522**, 523*, 524!, 568, 603
adunca, *670*
albicans, *496*
albicaulis, *499*
antillarum, *499*
apiahiensis, *538*
araucariae, *538*
asprella, *670*
aurea, *519*
bernoullii, *462*
bicolor, *499*
bipinnata, *370*
bogotensis, *388*
brunnescens, *604*
callicostata, *607*
capillata, *506*
carionis, *583*
caudifrons, *538*
chrysophyllopodia, *527*
ciliata, *469*
crispa, *658*
cruceana, *472*
cruegeriana, *628*
cubensis, *555*
cupressiformis, *533*
cuspidata, *504*
cymbifolia, *537*
densifolia, *499*
deppeana, *576*
depressa, *478*
diaphana, *565*
diffusa, *632*
divaricata, *544*
diversifolia, *527*
erythrochaete, *533*
falcata, *662*
fendleri, *504*
filescens, *651*
filiformis, *533*
flabellata, *272*
flexilis, *174*
glandulifera, *636*
gracilis, *665*
guadalupensis, *662*
haplociliata, *576*
hispidula, *441*
hospitans, *651*
hypnacea, *665*
incurva, *641*
intermedia, *588*
latifolia, *588*
leptorrhyncha, *533*
leucomioides, *673*
limbatula, *499*
lindigiana, *496*
lorifolia, *601*
magellanica, 522
membranacea, *278*
merkelii, *467*
muelleri, *576*
nicaraguensis, *496*
nitida, *620*
obliquicuspis, *506*
oerstediana, *469*
pallescens, *535*
pallida, *472*

Hookeria *(continued)*
pallidonitens, *578*
papillata, *538*
patrisiae, *484*
pendula, *646*
philonotula, *533*
pilifera, *538*
pilotrichelloides, *530*
pilotrichoides, *530*
planiuscula, *673*
polytrichoides, *583*
prasiophylla, *499*
pseudo-pilifera, *533*
pseudo-pilifera, *538*
punctata, *541*
purpureophylla, *648*
repens, *668*
riparia, *595*
rivularis, *651*
rorida, *506*
rubriseta, *509*
rufescens, *475*
splitgerberi, *486*
spruceana, *537*
striata, *519*
strumosa, *677*
subaurescens, *673*
subenervis, *586*
subfalcata, *670*
subfissidentoides, *651*
surinamensis, *592*
taylorii, *538*
tenera, *673*
tenuicuspis, *610*
tenuifolia, *601*
tenuis, *673*
tenuiseta, *546*
tuberculosa, *472*
ulophylla, *499*
undata, *658*
vaga, *636*
variabilis, *673*
varians, *514*
viridissima, *670*
weigeltiana, *472*
wrightii, *620*
Hookeriopsis, 444
sect. *Pseudo-Omaliadelphus*, *623*
sect. *Thamniopsis*, *623*
acicularis, *658*
angustiretis, *445*
bowersiana, *662*
callicostelloides, *464*
crispa, *658*
crosbyi, *449*
cruegeriana, *628*
cubensis, *636*
falcata, *662*
gracilis, *665*
guadalupensis, *662*
guatemalensis, *638*
heteroica, *665*
hospitans, *651*
hypnacea, *665*
killipii, *628*
laevinervis, *451*
leucomioides, *673*
maguirei, *628*
obtusifolia, *454*
panamensis, *464*
pendula, *646*
planiuscula, *673*
standleyi, *653*
steyermarkii, *656*
subaurescens, *673*
subfalcata, *670*
subfissidentoides, *651*
taylorii, *538*
tenera, *673*
tenuifolia, *601*
tenuis, *673*
tuberculosa, *472*
undata, *658*
variabilis, *673*
venezuelensis, *628*
viridissima, *670*
websteri, *458*
welchiana, *464*
Hylocomium
splendens, 383
Hylotapis, *525*
Hypnella, **525**
ambrosia, **527**, 528*
araucariae, *538*
brotheri, *530*
caudifrons, *538*
chrysophyllopodia, *527*
cymbifolia, *537*
diversifolia, 524!, **527**, 529*
erythrochaete, *533*
filiformis, *533*
guayanensis, **531**, 532*
leptorrhyncha, **533**, 534*
pallescens, **535**, 536*, 537!
philonotula, *533*
pilifera, 537!, **538**, 539*

pilotrichelloides, *530*
pseudo-pilifera, *533*
punctata, **541**, 542*
taylorii, *538*
wrightii, *620*
Hypnum
sect. *Catagonium*, *262*
sect. *Dendroglossophyllum*, *325*
sect. *Henicodium*, *189*
sect. *Omalia*, *267*
sect. *Pinnatella*, *311*
sect. *Thamnium*, *354*
subgen. *Thamnium*, *354*
acrophyllum, *679*
appressum, *127*
attenuatum, *3*
aureum, *519*
cirrifolium, 251
crispatulum, *151*
cuspidatifolium, *679*
defoliatum, *268*
densum, *91*
depressum, *478*
diaphanum, *565*
duplicatum, *184*
fasciculatum, *355*
flabellatum, *272*
flexile, *174*
flexuosum, *687*
glabellum, *268*
guadalupense, *662*
imbricatum, 307
lancifrons, *336*
leucotrichum, *138*
livens, *140*
mahahaicum, *322*
neckeraeforme, *336*
niam-niamiae, *190*
nigrescens, *127*
nigricans, *145*
patrisiae, *484*
patulum, *162*
pentastichum, 311
phryxophyllum, *519*
piniforme, *275*
polytrichoides, *583*
porotrichum, *339*
purpurascens, *35*
quadrangulare, *199*
rostratum, *7*
strumosum, *677*
tamarisci, *695*
tetragonum, *208*
trichophyllum, *170*
undatum, *658*
Hypopterygiaceae, **693**
subfam. *Cyathophoroideae*, *693*
trib. *Cyathophoreae*, *693*
Hypopterygiineae, *693*
Hypopterygium, **694**
cubense, *695*
pseudotamarisci, *695*
rigidulum, *695*
tamarisci, **695**, 696*, 697!
subsp. *pseudotamarisci*, *695*
tamariscinum, 697

Isodrepanium, **277**
lentulum, **278**, 279*, 280!
Isopterygiopsis, 262, 263
Isopterygium, 263, 702
brevicaudatum, *263*
machrisiorum, *700*
semicostatum, *86*
Isothecium
flexile, *174*
livens, *140*
nigricans, *145*
patulum, *162*
tetragonum, *208*
trichophorum, *105*

Jaegerina, 184, **192**, 242
guatemalensis, **193**, 194*, 195!
jamaicensis, *193*
scariosa, 189, **195**!, 196*, 245
Jaegerinopsis, *192*, 193
cubensis, *197*
ramosa, *318*
scariosa, *195*
squarrosa, *197*
ulei, *197*

Lembophyllaceae, **169**
Lembophyllum, 169
Lepidopilidium, **541**
divaricatum, **544**, 545*, 546!
nitens, 549
portoricense, **546**!, 547*
subdivaricatum, *544*
synoicum, *544*
tenuisetum, *546*
Lepidopilum, 435, **549**
sect. *Actinodontium*, *434*
sect. *Isodrepanium*, *277*

Lepidopilum *(continued)*
affine, **552**, 553*, 554!
amplirete, 554!, **55**5, 556*
antillarum, *558*
antisanense, *552*
apiculatum, *555*
attenuatum, *580*
aureofulvum, *572*
biductulosum, 595
brevipes, **558**, 559*, 560!
calomicron, *482*
carionis, *583*
carneum, *590*
cladorrhizans, *572*
contiguum, *592*
crassisetum, *576*
crispifolium, *595*
cubense, *555*
curvifolium, 560!, **561**, 562*
cuspidans, **563**, 564*, 565!
decaisnei, *558*
var. *brevicuspis*, *558*
denticulatum, *511*
deppeanum, *576*
diaphanum, **565**!, 566*
divaricatum, *544*
dominicense, *588*
epiphyllum, *482*
excelsum, *583*
exiguum, **568**, 569*, 570!
falcatulum, *588*
filiferum, *588*
flaccidissimum, *482*
flexifolium, 595
floresianum, *576*
gertrudis, *561*
haplociatum, *576*
herminieri, *486*
herzogii, *574*
huallagense, *565*
imbricatifolium, *700*
incurvum, *641*
inflexum, **570**!, 571*
integerrimum, *572*
integrifolium, *436*
intermedium, *588*
laetenitens, *558*
latifolium, *588*
livens, *588*
longifolium, 440, **572**, 573*, 574!
membranaceum, *278*
mnioides, *583*
muelleri, 574!, **576**, 577*
pallidonitens, **578**, 579*, 580!
patrisiae, *484*
permarginatum, 580!, **581**, 582*
phyllorhizum, *555*
platyphyllum, *583*
polytrichoides, **583**, 584*, 585!
var. *costa-ricense*, *583*
var. *pellucens*, *583*
portoricense, *546*
pringlei, *576*
quadrifarium, *578*
radicale, *588*
robustum, *572*
rotundifolium, *561*, 595
scabrisetum, 585!, **586**, 587*
semilaeve, *555*
skutchii, *555*
splitgerberi, *486*
sprucei, *436*
steyermarkii, *592*
stillicidiorum, **590**, 591*, 592!
stolonaceum, *588*
subdivaricatum, *544*
subenerve, *586*
subepiphyllum, *486*
subpolytrichoides, *583*
subtortifolium, *511*
surinamense, **592**!, 593*
tortifolium, 509, 513, **595**, 596*, 597!
ultramarginatum, 597!, **598**, 599*
undatum, *658*
vesicularioides, *565*
Leptodon, 75
Leptodontaceae, 90
Leptohymenium
tenue, 325
Lepyrodontaceae, **85**
Lepyrodon, **85**, 170
duellii, *86*
lagurus, 88
tomentosus, **86**, 87*, 88!
var. *latifolius*, *86*
trichophyllus, *170*
fo. *robustior*, *172*
var. *robustior*, *172*
var. *subtilis*, *172*
Lepyrodontopsis, **169**
trichophylla, 167!, **170**, 171*
Leskea, 1, 419
subgen. *Omalia*, *267*
subgen. *Hemiragis*, *518*
aciculata, *102*
albicans, *496*
attenuata, *3*
debilis, *112*
decomposita, *272*
depressa, *478*

flabellata, *272*
flexilis, *121*, *174*
glabella, *268*
heteroclados, *107*
imponderosa, *148*
remotifolia, *115*
rostrata, *7*
striata, *519*
superba, *320*
tamariscina, 698
tristis, *10*
undata, *658*
Leskeodon, **418**
andicola, 417!, **419**, 420*
auratus, **422**, 423*, 424!
caducifolius, *427*
cubensis, **424**!, 425*
elongatus, *424*
longipilus, *424*
mariei, *427*
mexicanus, *419*
paisa, **427**, 428*, 429!
palmarum, **427**, 429!, 430*
pusillus, *422*
Leucodontaceae, **78**
Leucodon, 66, **78**
sect. Macrosporiella, 79
subgen. Cryptotheca, 79
subgen. Leucodontella, 79
brachypus, **79**, 80*, 81!
cryptotheca, 83
curvirostris, **81**!, 82*
domingensis, *75*
flagellaris, *75*
geniculatus, *190*
julaceus, 81
macrosporus, *81*
pohlii, *233*
tomentosus, *86*
trichophyllus, *170*
Leucodontella, 78, 79
brachypus, *79*
Leucodontopsis, *189*
floridana, *190*
geniculata, *190*
plicata, *190*
Leucomiaceae, **676**
Leucomium, 675, **677**
acrophyllum, *679*
attenuatum, *679*
compressum, *679*
connexum, *679*
costaricense, *679*
cuspidatifolium, *679*
cuspidatum, *679*
flexuosum, *687*
guianense, *679*
latifolium, *679*
mariei, *679*
mosenii, *679*
mouretii, *679*
robustum, *679*
scabrum, *679*
strumosum, 603, 675!, **677**, 678*
Levierella, 387
Lindigia, 102, **111**
aciculata, *102*
capillacea, *102*
curtipes, *112*
debilis, 105, 111!, **112**, 113*
pilotrichelloides, *112*
tenella, *102*
Lophidiaceae, *693*
Lopidium, 693
Loxotis, *147*
imponderosa, *148*

Macromitrium, 250, 600, 655
Mesotus, 66
Meteoriaceae, **100**
Meteoridium, **114**
remotifolium, **115**, 116*, 117!, 165
tenuissimum, **117**!, 118*
Meteoriopsis
sect. *Meteoridium*, *114*
sect. *Squarridium*, *157*
ambiguum, *160*
patula, *162*
var. *congesta*, *162*
recurvifolia, *165*
remotifolia, *115*
Meteorium, **120**
sect. *Papillaria*, *120*
sect. *Squamidium*, *132*
sect. *Squarridium*, *157*
sect. *Trachypus*, *154*
aciculatum, *102*
ambiguum, *160*
appressum, *127*
capillaceum, *102*
cochlearifolium, *174*
cubense, *107*
debile, *112*
deppei, 109, **121**, 122*, 123!, 168
diclados, *107*
enerve, *107*
excavatum, *199*
filiferum, *140*
flaccidum, *109*
flexile, *121*, *174*

Meteorium *(continued)*
guyanense, *199*
illecebrum, *121*
var. *gracile*, *123*
imponderosum, *148*
laevifolium, 123!, **125**, 126*, 168
leucotrichum, *138*
livens, *140*
macrocarpum, *142*
mauiensis, *178*
mexicanum, *246*
nigrescens, **127**, 128*, 129!
nigricans, *145*
oerstedianum, *148*
orbifolium, *176*
papillarioides, 130
patulum, *162*
penicillatum, *168*
pseudoteres, *123*
recurvifolium, *165*
remotifolium, *115*
scariosum, *195*
sericeum, *172*
sinuatum, *121*
tenuissimum, *117*
teres, 129!, **130**, 131*
tetragonum, *208*
trichophoroides, *107*
trichophorum, *105*
turgescens, *174*
undulifolium, *123*
viridulum, *154*
vulcanicum, *178*
wagneri, *160*
Miyabea, 1
Mniadelphus
andicola, *419*
auratus, *422*
bogotensis, *388*
cubensis, *424*
geheebii, *388*
palmarum, *427*
pusillus, *422*
Mnium
aureum, *519*
Monocryphaea, *39*, 40
ravenelii, *40*
Monoschisma, *120*
viride, *121*
Muelleria, 66

Neckeraceae, **266**
subfam. *Thamnioideae*, *266*
Neckera, **281**
sect. *Cryphidium*, *39*
sect. *Cryptopodia*, *281*
sect. *Leucodon*, *78*
sect. *Omalia*, *267*
sect. *Paraphysanthus*, *292*
sect. *Pseudopilotrichum*, *300*
sect. *Taeniocladium*, *292*
sect. *Thamnium*, *354*
subgen. *Pilotrichum*, *364*
subsect. *Meteoridium*, *114*
subsect. *Orthostichella*, *300*
subsect. *Papillaria*, *120*
subsect. *Paraphysanthus*, *292*
subsect. *Taeniocladium*, *292*
aciculata, *102*
acutifolia, *184*
ampullacea, *306*
appressa, *127*
biformis, *322*
bipinnata, *370*
bogotensis, *287*
capillacea, *102*
chilensis, 280!, **282**, 283*
chlorocaulis, *284*
cochlearifolia, *174*
crispatula, *151*
cymbifolia, *217*
debilis, *112*
decomposita, *272*
densa, *91*
deppei, *121*
disticha, *293*
diversicoma, *133*
domingensis, *75*
dubyana, *121*
duplicata, *184*
ehrenbergii, **284**, 285*, 286!
falcifolia, *278*
fasciculata, *355*
filifera, *140*
filiformis, *45*
flabellata, *272*, *342*
flexilis, *174*
floridana, *190*
foveolata, *296*
fusco-viridis, *123*
glabella, *268*
guayanensis, *199*
hornschuchiana, *284*
humboldtii, *35*
illecebra, *121*
jamesonii, *282*
korthalsiana, *333*
lentula, *278*
liebmanniana, *22*
lindigii, *287*

livens, *140*
longipes, *233*
longirostre, *339*
ludoviciae, *233*
ludoviciana, *233*
luteovirens, *97*
microcarpa, *289*, *292*
mohriana, *272*
nigrescens, *127*
nigricans, *145*
novae-granadae, *282*
oerstediana, *148*
pachygaster, *307*, 310
var. *gracilis*, *307*
patula, *162*
pohlii, *233*
polytrichoides, *583*
porodictyon, *184*
remotifolia, *115*
retusa, *293*
rigida, *304*
scabridens, 286!, **287**, 288*
scabriseta, *586*
scalpellifolia, *272*
secunda, *20*
sinuata, *121*
sphaerocarpa, *22*
substriata, *345*
tetragona, *208*
tomentosa, *86*
trichophora, *105*
trichophoroides, *107*
trichophylla, *170*
turgescens, *174*
undulata, *298*
urnigera, **289**, 290*, 291!
versicolor, *307*
viridis, *121*, *307*
viridula, *154*
wercklei, *289*
Neckeropsis, **292**
sect. *Paraphysanthus*, *292*
sect. *Taeniocladium*, *292*
crinata, 300
disticha, 291!, **293**, 294*
folveolata, **296**, 297*, 298!
undulata, **298**!, 299*
Neobarbella, 169
Neodicladiella, 105
Neohypnella, *525*
chrysophyllopodia, *527*
diversifolia, *527*
mucronifolia, *530*
Neolindbergia, 90
flagellifera, *236*
Ochrobryum, 610
Omalia, *267*
glabella, *268*
Orthorrhynchidium, *183*
planifrons, *187*
Orthostichella, 173, 292, **300**
anacamptacea, *145*
capillicaulis, 304
filamentosula, *307*
hexasticha, 307
longinervis, 307
muelleri, 304
pachygastrella, **302**, 303*, 304!
pentasticha, *311*
rigida, **304**!, 305*
versicolor, **307**, 308*, 309!
viridis, *307*
welwitschii, 311
Orthostichidium, **198**
excavatum, *199*
guyanense, *199*
involutifolium, 198, 202
pentagonum, *199*
pentasticum, 198
quadrangulare, **199**, 200*, 201!, 210, 238, 245, 311
tetragonum, *208*
Orthostichopsis, **202**
auricosta, 207
fornicata, 201!, **203**, 204*
praetermissa, **205**, 206*, 207!, 311
tenuis, 311
tetragona, 202, 207!, **208**, 209*
Orthothecium
trichophyllum, *170*
Orthotrichum
concavifolium, *58*
polytrichoides, *583*

Palamocladium, 170
leskeoides, 173
trichophyllum, *170*
var. *subtilis*, *172*
Papillaria, *120*, 148
sect. *Floribundaria*, *108*
sect. *Trachypus*, *153*
appressa, *127*, 130
crispatula, *151*
deppei, *121*
diversicoma, *133*
dubyana, *121*
flaccida, *109*
flexilis, *121*
fusco-viridis, *123*
illecebra, *121*

Papillaria (continued)
imponderosa, *148*
laevifolia, *125*
leuconeura, *130*
longifolia, *156*
nigrescens, *127*
subsp. *donellii*, *127*
var. *donnellii*, *127*
oerstediana, *148*
penicillata, *168*
sinuata, *121*
squamatula, *125*
teres, *130*
viridula, *154*
warszewiczii, 168
Paraphysanthus, *292*
Pararhacocarpus, 31
Philophyllum, **600**
bromeliae, *601*
bromeliophilum, *601*
lorifolium, *601*
tenuifolium, **601**, 602*, 603!
Phyllodon, 702
truncatulus, 702
Phyllodrepanium
falcifolium, 281
Phyllogoniaceae, **252**
Phyllogonium, **252**
aureum, *253*
fulgens, 250!, **253**, 254*
var. *gracile*, *255*, 256
var. *rufescens*, *255*, 256
var. *viride*, *256*
var. *viscosum*, *259*
globitheca, *255*
goebelii, *255*
serra, *259*
speciosum, *259*
viride, **256**, 257*, 258!
viscosum, 177, 186, **258**!, 260*
var. *viride*, *256*
Piloseriopus, *391*
haitensis, *392*
Pilotrichaceae, **363**
Pilotrichella, 100, 169, **173**
sect. *Eupilotrichella*, *173*
sect. *Gastrella*, *173*
sect. *Meteoridium*, *114*
sect. *Papillaria*, *120*
sect. *Turgidella*, *173*
allionii, *309*
ampullacea, *306*
angustifolia, *309*
cochlearifolia, *174*
var. *flagellifera*, *178*
cubensis, *107*
cymbifolia, *217*
cyathipoma
var. *laxiretis*, *302*
deppei, *121*
desmoclada, *178*
dubyana, *121*
eroso-mucronata, *176*
excavata, *199*
filamentosula, *307*
filifera, *140*
flagellifera, *178*
flexilis, 65, 147, **174**, 175*, 176!, 251, 261
fo. nudiramosa, 175*, 176!, **178**
var. *robusta*, *176*
floridana, *190*
fusco-viridis, *121*
guyanensis, *199*
illecebra, *121*
imponderosa, *148*
isoclada, *136*
leucotricha, *138*
livens, *140*
longifolia, *156*
longipes, *233*
ludoviciana, *233*
mauiensis, **178**, 179*, 180!
mexicana, *306*
nana, *231*
nigricans, *145*
nudiramulosa, *178*
pachygaster, *307*
var. *gracilis*, *307*
pachygastrella, *302*
pentagona, *199*
pentasticha, *311*
pohlii, *233*
pulchella, *306*
recurvo-mucronata, *176*
remotifolia, *115*
rigens, *176*
rigida, *304*
sinuata, *121*
tenuinervis, *145*
tenuissima, *117*
teres, *130*
tetragona, *208*
tonduzii, *233*
trichophora, *107*
trichophoroides, *107*
turgescens, *174*
versicolor, *307*
viridis, *307*
Pilotrichidium, **603**
antillarum, 603!, **604**, 605*
var. *complanatum*, *604*
var. *cubense*, *604*

brunnescens, *604*
callicostatum, 461, 469, **607**, 608!, 609*
Pilotrichopsis, 54
Pilotrichum, **364**
sect. *Cryphaea*, *39*
sect. *Lepidopilum*, *549*
sect. *Pterobryon*, *239*
subgen. *Meteorium*, *120*
amazonum, *375*
ambiguum, *160*
andersonii, **365**, 366*, 367!
angustifolium, *212*
asperifolium, 367!, **368**, 369*
bipinnatum, **370**, 371*, 372!
var. *evanescens*, *375*
var. *filinerve*, *367*
capillaceum, *102*
cochlearifolium, *174*, *246*
corrugatum, 372!, **373**, 374*
cryphaeoides, *375*
cymbifolium, *217*
delicatulum, *381*
densum, *239*
distichum, *293*
dubium, *375*
evanescens, **375**, 376*, 377!
fasciculatum, *378*
fendleri, 377!, **378**, 379*
filicinum
var. *longipes*, *233*
filiferum, *140*
filiforme, *45*
filigranum, *381*
flagelliferum, *75*
flexile, *121*, *174*
hornschuchii, *239*
illecebrum, *121*
imponderosum, *148*
julaceum, *61*
lindigii, *318*
longipes, *233*
ludoviciae, *233*
mucronatum
var. *elongatum*, *378*
nigricans, *145*
nitidum, *322*
nivale, *25*
obtusatum, *373*
pallidum, *378*
patulum, *162*
pentagonum, *199*
piniforme, *275*
polytrichoides, *583*
ramosissimum, **381**, 382*, 383!
recurvifolium, *165*
rufescens, *54*
rugifolium, **383**!, 384*
scabridum, *375*
scabrisetum, *586*
scariosum, *195*
sinuatum, *121*
spiculiferum, *375*
subrevolutum, *25*
tonduzii, *378*
trinitense, *375*
undulatum, *298*
Pilotrichopsis, 38
Pinnatella, **311**
jamaicensis, *312*
minuta, 309!, **312**, 313*, 327
paraguayensis, *312*
piniformis, *275*
usagara, *351*
Pirea, *210*
cavifolia, *318*
cymbifolia, *217*
filicina, *222*
ludoviciae, *233*
mariae, *229*
pachyclada, *236*
papillosula, *231*
pohlii, *233*
tonduzii, *233*
Pireella, 198, **210**, 239
angustifolia, **212**, 213*, 214!
cavifolia, *318*
crosbyi, 214!, **215**, 216*
cubensis, *236*
cymbifolia, **217**, 218*, 219!
denticulata, *217*
falcifolia, **219**!, 220*
filicina, **222**, 223*, 224!
guatemalensis, **224**!, 225*
var. *mexicana*, *224*
hondurensis, **226**, 227*, 228!
ludoviciae, *233*
mariae, 228!, **229**, 230*
pachyclada, *236*
panamensis, *222*
papillosula, **231**, 232*, 233!
pergemmescens, 217
pohlii, 201, **233**!, 234*
pycnothallodes, **236**, 237*, 238!, 245
squarrosa, *347*
tonduzii, *233*
Plagiothecium, 263, 682, 692
Pleurozium schreberi, 325
Pohlia, 181
Porophyllum longirostrum, *339*
Porothamnium, 316, *325*
crassipes, *336*
decompositum, *272*

Porothamnium (continued)
fasciculatum, *355*
lancifrons, *336*
molliculum, *351*
natalense, *351*
neckeraeforme, *336*
substriatum, *345*
Porotrichodendron, **315**
bertrandii, **316**, 317*, 318!
biforme, *322*
bolivianum, *322*
filiferum, *322*
flavidulum, *322*
glaziovii, *322*
gracile, *322*
lindigii, **318**!, 319*
longipes, *324*
mahahaicum, *322*
nitidum, *322*
porteri, *324*
robustum, *322*
substolonaceum, *322*
superbum, **320**, 321*, 322!, 323*
Porotrichum, 316, **325**
sect. *Pinnatella*, *311*
sect. *Thamnium*, *354*
bertrandii, *316*
brevifolium, 315, 322!, **327**, 328*
caudatum, *349*
cavifolium, *318*
cobanense, *333*
crassipes, *336*
crassipes, 339
decompositum, *272*
evansii, **329**, 330*, 331!, 358
fasciculatum, *355*
filiferum, *322*
filiferum, **331**!, 332*
flabellatum, *272*
flavidulum, *322*
glaziovii, *322*
grandidens, *272*
var. *domingense*, *272*
guatemalense, *351*
insularum, *342*
korthalsianum, **333**, 334*, 335!
lancifrons, 335!, **336**, 337*
leavenworthii, *351*, 354
lindigii, *318*
longirostre, **339**, 340*, 341!
mexicanum, *339*
minutum, *312*
molliculum, *351*
mutabile, 341!, **342**, 343*
natalense, *351*
neckeraeforme, *336*
paraguayense, *312*
piniforme, *275*
pittieri, **345**, 346*, 347!
plagiorhynchum, *339*, 342
plicatulum, *347*
plumosum, *239*, 242
porteri, *324*
pringlei, *342*
scalpellifolium, *272*
squarrosum, *347*
substolonaceum, *322*
substriatum, 315, **345**, 347!, 348*
tenuinerve, **349**, 350*, 351!
usagarum, **351**!, 352*
variabile, *342*
Prionodontaceae, **90**
Prionodon, **90**, 242
arsenei, *93*
bolivianus, 99
caldensis, *91*
contortus, *93*
densus, 88!, **91**, 92*
var. *crispatulus*, *93*
var. *luteovirens*, *97*
dichotomus, *91*, 94
fragilifolio, 99
fuscolutescens, **94**, 95*, 96!
hoffmannii, 99
jamesonii, *97*
laeviusculus, *97*
longissimus, *97*
longissimus, 99
luteovirens, 96!, **97**, 98*
mexicanus, *93*
nitidulans, *91*
otiophylla, *153*
solorzanoi, *97*
splendens, *239*
undulatus, *91*
Pseudocryphaea, **74**
domingensis, 72!, **75**, 76*, 192
flagellifera, *75*
Pseudohypnella, 526
guianensis, *537*
mucronifolia, *530*
Pseudopilotrichum, 173, *300*
Pseudotaxiphyllum, 262, 702
distichaceum, 702
elegans, 181
machrisiorum, *700*
Pterigynandrum
domingense, *75*
fulgens, *253*
var. *viscosum*, *258*

nigrescens, *127*
viscosum, *258*
Pterobryaceae, 85, **182**
Pterobryon, **239**
sect. *Calyptothecium*, *183*
subgen. *Calyptothecium*, *183*
angustifolium, *212*
fo. *flagelliferum*, *212*
var. *flabelliforme*, *212*
var. *flagelliferum*, *212*
cymbifolium, *217*
densum, 215, 238!, **239**, 240*
var. *condensatum*, *239*
var. *peracuminatum*, *239*
duplicatum, *184*
filicinum, *222*
integrifolium, *212*
ludoviciae, *233*
panamense, *239*, 241
pohlii, *233*
Pterobryopsis, **242**
sect. *Eupterobryopsis*, *242*
sect. *Pseudo-Calyptothecium*, *183*
sect. *Pterobryodendron*, *242*
acutifolium, *184*
mexicana, 201, **243**, 244*, 245!
pringlei, *243*
scariosa, *195*
stolonacea, 245
subcochlearifolia, *176*
subfrondosa, *243*
ulei, *197*
Pterobryum cochlearifolium, *246*
Pterogoniadelphus, 78
Pterogonium
densum, *91*
fulgens, *253*
nigrescens, *127*
viscosum, *259*
Pterygophyllum
acutifolium, *522*
albicans, *496*
bogotense, *388*
decompositum, *272*
depressum, *478*
diaphanum, *565*
falcatum, *662*
undatum, *658*
Ptychomniaceae, 85
Pylaisia selwynii, 94

Racomitrium lanuginosum, 27
Racopilum, 698
Renauldia, 199, 242, **245**
cochlearifolia, *246*
dusenii, 251
mexicana, 198, 202, 245!, **246**, 247*
paradoxica, **248**, 249*, 250!
Rhacocarpaceae, **31**
Rhacocarpus, **31**
apiculatus, **33**, 34*, 35!
chlorotus, 32
inermis, 33
purpurascens, **35**!, 36*
squamosus, *33*
Rhacopilopsis, 698
Rhynchostegiella, 102
capillacea, *102*
Rhynchostegiopsis, 675, **681**
auricolor, *687*
carolae, **682**, 683*, 684!
complanata, *690*
costaricensis, 684!, **685**, 686*
cupressina, *687*
flexuosa, **687**, 688*, 689!
lutescens, *690*
planifolia, *690*
tunguraguana, 689!, **690**, 691*
Rhynchostegium, 115, 117
cupressinum, *687*
scariosum, 105
Rhystophyllum, *281*
distichum, *293*

Schimperobryum, 522
Schistophyllum dominicense, *184*
Schizomitrium, *460*
aquaticum, *472*
bernoullii, *462*
ciliatum, *469*
colombicum, *625*
depressum, *478*
grossirete, *625*
guatemalense, *638*
hondurense, *467*
merkelii, *467*
oerstedianum, *469*
pallidum, *472*
rivulare, *651*
rufescens, *475*
subfissidentoides, *651*
tenerrimum, *625*
vatteri, *467*
Schliephackea, 250
Schoenobryum, 16, **57**
coffeae, *58*, 60
concavifolium, 57!, **58**, 59*
gardneri, *58*
julaceum, **61**, 62*, 63!
var. *costaricensis*, *58*

Schoenobryum *(continued)*
mittenii, *63*
rubricaule, **63**!, 64*
Sematophyllaceae, 526
Sematophyllum subpinnatum, 192
Sorapilla, 252
Sphaerotheciella, **65**
gracillima, **66**, 67*, 68!
macrospora, 66
pachycarpa, **68**!, 69*
pinnata, **70**, 71*, 72!
Spiridentopsis longissima, 251
Squamidium, **132**, 173
sect. Macrosquamidium, 133
sect. Squamidium, 133
chiriquense, *135*
crispipilum, *142*
cubense, *107*
diversicoma, **133**, 134*, 135!
diversifolium, *133*
filiferum, *140*
isocladum, 135!, **136**, 137*
leucotrichum, 124, **138**, 139*, 140!
livens, **140**!, 141*
macrocarpum, **142**, 143*, 144!
nigricans, 144!, **145**, 146*, 177, 311
tenuinerve, *145*
Stenodesmus, **609**
tenuicuspis, 609!, **610**, 611*
Stenodictyon, 435, **612**
bisodalense, *574*, 622
crosbyi, **614**, 615*, 616!
nitidum, *620*
ovatum, **616**!, 617*
pallidum, 601, **618**, 619*
sericeum, *620*
wrightii, **620**, 621*, 622!
Stereodon
tunguraguanus, *690*
Symphyodontaceae, **699**
Symphyodon, **699**
americanus, *700*
imbricatifolius, 697!, **700**, 701*
pygmaeus, 700
Syrrhopodon, 387

Taiwaniobryum, 90
Taxicaulis andino-subulatus, *170*
Taxiphyllum, 702
laevifolium, 702
machrisiorum, *700*
Taxithelium, 526
Tetrastichium, 676
Thamniaceae, *266*
Thamniopsis, **623**
colombica, 622!, **625**, 626*
cruegeriana, **628**, 629*, 630*, 631!
diffusa, 631!, **632**, 633*, 634*
glandulifera, **636**, 637*, 638!
guatemalensis, 464, **638**!, 639*
incurva, **641**, 642*, 643!
killipii, *628*
oedodontia, **643**!, 644*
pendula, **646**, 647*, 648!
purpureophylla, **648**!, 649*
rivularis, **651**, 652*, 653!
standleyi, **653**!, 654*
steyermarkii, **656**, 657*, 658!
undata, 514, **658**!, 659*
Thamnium, *354*
sect. *Trachyphylla*, *325*
subgen. *Porotrichum*, *325*
cobanense, *333*
decompositum, *272*
fasciculatum, *355*
filiferum, *331*
flabellatum, *272*
lancifrons, *336*
longirostre, *339*
mexicanum, *339*
molliculum, *351*
natalense, *351*
neckeraeforme, *336*
piniforme, *275*
pittieri, *345*
plagiorhynchum, *339*
plicatulum, *347*
substriatum, *345*
toccoae, *13*
tumidicaule, *360*
variabile, *342*
Thamnobryaceae, *266*
Thamnobryum, 32, **354**
fasciculatum, **355**, 356*, 357!
liesneri, **358**, 359*
tumidicaule, 357!, **360**, 361*
Thelia, 1
Toloxis, **147**
imponderosa, 130, **148**, 149*, 150!, 168
semitorta, 148
Trachyphyllum, 387
Trachypodium subenerve, *588*
Trachypodopsis, 148, **151**
auriculata, 151
crispatula, *153*
otiophylla, *153*
serrulata, 151
var. crispatula, 150!, **151**, 152*
Trachypus, **153**
bicolor, 157
var. viridulus, 150, 153, **154**, 155*, 156!, 168

crispatulus, *151*
viridulus, *156*, 157
Trachythecium, 699
Trachyxiphium, **661**
aduncum, *670*
glanduliferum, *636*
guadalupense, **662**, 663*, 664!
heteroicum, *665*
hypnaceum, 664!, **665**, 666*
repens, **668**, 669*, 670!
subfalcatum, **670**!, 671*
tenue, *673*
vagum, *636*
variabile, **673**, 674*, 675!
Tricholepis, *120*
nigrescens, *127*
var. *donnellii*, *127*
Tristichium, 387
Unclejackia, 699
Vesicularia, 111, 677, 682
sect. *Rhynchostegiopsis*, *681*
auricolor, *687*
strumosa, *677*
vesicularis, 680, 690
Vesiculariopsis, 676
Weymouthia, 100, 169, 173
desmoclada, *178*
Zelometeorium, 114, **157**
allionii, 156!, **158**, 159*
ambiguum, **160**, 161*, 162!
patulum, 109, **162**!, 163*
recurvifolium, **165**, 166*, 167!

Bruce Allen is a bryophyte curator at the Missouri Botanical Garden. His principal research interest is floristics. He is presently working on part four of the *Moss Flora of Central America* as well as part two of a moss flora of Maine. He also maintains an active interest in revisionary studies on a wide range of moss groups.

Line illustration: *Pilotrichella flexilis* (Hedw.) Ångstr.

Missouri Botanical Garden Press
P.O. Box 299
St. Louis, Missouri 63166-0299
www.mbgpress.org

Cover design by Gobberdiel Strategic Communications,
St. Louis, Missouri.

Printed in the U.S.A.

ISBN 978-1-930723-95-5